An Introduction to the Ecology and Behaviour of the Prawn, *Palaemon affinis* Milne-Edwards, 1837 (Crustacea: Decapoda: Natantia)

A thesis

submitted in partial fulfillment

of the requirement for the Degree

of

Masters of Science in Zoology

in the

University of Canterbury

by

Courtney A Day

University of Canterbury

2001

Table of Contents

Abstract

Palaemon affinis is the commonest prawn in intertidal habitats of the North and South Islands, New Zealand. The population dynamics, community composition, and natural food preferences of *P. affinis* were studied in the Avon-Heathcote Estuary, and rock pools at Taylors Mistake and Kaikoura, South Island, in 2000. Bimonthly samples were taken at all three sites at low tide using a suction sampler for the hyperbenthic communities and a corer or quadrat for the benthic communities. The distribution of *P. affinis* was patchy and its abundance fluctuated seasonally, peaking at the estuary and Kaikoura in winter (≥580 individuals per m^2) and at Taylors Mistake in autumn (294 individuals per m^2).

The carapace length (CL, mm), total body length (TBL, mm), and wet weight (W, g) of *P. affinis* were measured. Males were 15-19 mm CL, 19-50 mm TBL, 0.060-1.091 g W, and females were 5-21 mm CL, 13-54 mm TBL and 0.021-1.691 g W. The size ranges differed between the populations. Males from Kaikoura grew at a slower rate than females (CL against TBL or W), but not those from the Culvert or Taylors Mistake. There were no differences in growth rate between males and females for pooled data. For the pooled samples, males were significantly smaller/larger than females in TBL, but not in CL or W. The sex ratios were skewed: males dominated the medium size class (9-14 mm CL at the Culvert and Taylors Mistake; 9-12 mm CL at Kaikoura), and females the large size class (15-21 mm CL at the Culvert and Taylors Mistake, 13-15 mm CL at Kaikoura).

The breeding season of *P. affinis* was in spring and summer, but the time when ovigerous females first appeared differed between populations. Size at onset of maturity for females in the pooled data was 13 mm CL, but the size differed between sites. Ovigerous female were 13-20 mm CL, 33-53 mm TLB, and 0.370-1.729 g W and carried 110-690 eggs that weighed 0.033-0.260 g W. There was no relationship between female body size and fecundity (number eggs), perhaps because of low sample size.

The communities at the three sites shared 8 species in common: 2 molluscs (*Melagraphia aethiops* and *Notoacmea* sp.), 2 polychaetes (*Haploscoloplos cylindrifer* and Nereidae), a crab (*Halicarcinus varius*), an amphipod (Gammaridae), an isopod (Sphaeromatidae), and a brittle star (*Amphiura hinemoa*). Gammarid amphipods and *P. affinis* itself contributed most to the similarity index for within-population analysis and to the dissimilarity between populations. Environmental variables (minimum/maximum water depth, water temperature, substratum, site size, salinity) were not well correlated with community composition. At Taylors Mistake, salinity was important (~ 89% similarity), but substratum type was responsible for most of the similarity (~51% similarity) between communities.

Contrary to expectation, *P. affinis* was mainly carnivorous. Gammarid amphipods were the main food item which was found in ~ 71% of *P. affinis* stomachs. Other items included unidentifiable matter, polychaetes, molluscs, plant material, ostracods, isopods, sand grains, sponge spicules and crab. No difference in diet between sexes, size classes or seasons was found. Low fullness values were found with only ~28% of 264 stomachs ≥50% full.

Periodicity in the locomotor and feeding activities of *P. affinis* from Kaikoura were examined in laboratory experiments in tanks provided with a continuous supply of fresh flowing seawater. Prawns were recorded using a 24 h time-lapse video camera under constant (red) light. To test for the effect of tide on locomotion, two experiments were conducted with artificial tide cycles simulating natural tide cycles at Kaikoura under constant light (water temperature, 12 ± 1°C), and under constant darkness (water temperature, 20 ± 2.5°C). The effects of day-night cycles on locomotion used a 12 h light: 12 h dark regime with a constant (low) tide (7 cm water depth) at 14.5 ± 2°C. Feeding experiments were conducted using both a simulated 25 h tidal cycle and a 12 h light: 12 h dark regime (water temperature 19.5 ± 1.5°C). Diel and circatidal rhythms in locomotor activity were found, with maximum activity at night and at high tide. No rhythmicity was found in the feeding activity of *P. affinis*.

List of Plates

List of Figures

List of Tables

Chapter One

General Introduction

Chapter One: General Introduction

1.1. Background

Survival of a prawn, as an individual or as the species, depends on its being adapted to its environment. Key adaptations, such as growth and reproduction, are affected by a multitude of environmental factors, most especially food resources, breeding sites, refugia, competition, and predator avoidance (Stearns 1976). How successful a species is through time depends on how well it copes with its physiological and structural limitations with respect to the demands of its environment (Meglitsch 1972; Stearns 1976). In this thesis, I report on aspects of biological and behavioural adaptations that determine the habitat of the common New Zealand intertidal prawn, *Palaemon affinis* Milne-Edwards, 1837.

The Crustacea include groups that exhibit several types of growth patterns and reproductive strategies (Hartnoll 1985). Regardless of the structure and strategy, any species needs energy to support its long-term growth and reproduction, as well as daily activities, such as searching for food, shelter, or a mate, and avoiding predators. The use of energy for one activity denies its use for another; so there is always a trade-off in the allocation of energy. However, evolutionary theory predicts that energy resources will be used to maximise the net reproductive output (Stearns 1976).

Before considering adaptations to the environment, it is useful to summarise some aspects of general crustacean biology to set out the common constraints on structural and physiological adaptations of the crustacean body plan. Crustacea are characterised by a hard exoskeleton that typically prevents any increase in size or growth without shedding, moulting or ecdysis. The periods between moults are referred to as stages or instars (Green 1961; Hartnoll 1985). In most groups, physical growth can only occur immediately after moulting, when the new exoskeleton is still soft and extensible (Green 1961) and the new tissue formed during the instar life can be expanded into an ~~expanded~~ new & larger exoskeleton. Thus, the growth rate of most crustaceans is determined by any increase in size at each moulting. Growth rates vary between instars, but generally, as the animal increases in size, the number of moults decreases and the duration of the instar increases (Green 1961; Hartnoll 1985). Growth rates commonly vary between sexes as well. Sexual dimorphism in growth typically becomes apparent after the animal is sexually mature (Ra'anan & Cohen 1985). The

growth pattern used by any species or either sex is affected by environmental variables (Stearns 1976).

Reproduction is also affected by moulting. In most Crustacea, the reproductive process involves copulation, followed by laying and incubation of eggs. Copulation is often only possible immediately after the female has moulted. Female Crustacea will generally release their entire production of ova during a single laying event and the ovary must mature again before further eggs can be laid. Therefore, the transference of spermatozoa from the male to the female during copulation typically fertilises a single batch of eggs. Once the female moults, it is common for the spermatozoa from the previous copulations to be lost. The combined processes result in many Crustacea producing only one batch of eggs per instar. Most ~~Crustacea~~ Decapoda retain the eggs and incubate them beneath the abdomen until they hatch; both these factors result in all eggs hatching at one time (Hartnoll 1985).

Competition in the allocation of energy and physical resources between growth and reproduction is inevitable (Stearns 1976; Hartnoll 1985). In addition, changes in behaviour associated with reproduction, such as courtship displays in males or incubating behaviour in females, may alter feeding activities, and hence affect energy and nutrient intake. Indeed, incubating females may reduce or cease feeding altogether (Green 1961; Hartnoll 1985; Ra'anan & Cohen 1985). Even if sufficient energy resources are available for both growth and reproduction, moulting may be delayed because of the time required for incubation. Conversely, growth may be advantageous for overall net reproduction. As noted above, many females incubate their eggs beneath the abdomen, so a larger female may be able to carry more eggs than a smaller female. Even though female size may determine the number of offspring she contributes to future generations, the energy and nutrients that are put into reproduction are not available for growth so there must be a trade off in the allocation of resources. Reproduction can never enhance growth, but must always inhibit it (Hartnoll 1985). The strategy employed by a particular species should, according to the evolutionary theory, be one that maximises the number of offspring surviving to the next generation (Stearns 1976). A larger female prawn may produce more eggs, but the time taken to achieve that size may delay breeding until environmental factors such as temperature reduces the viability of the offspring.

There must also be a trade off in egg size with greater number, which might also affect the viability of the young; a female can either produce a few large eggs, or more smaller eggs (Hartnoll 1985).

Within the Crustacea in general, several modes of growth and reproduction have evolved, but they can be grouped into two main categories: indeterminate and determinate growth. Only strategies involving indeterminate growth are important here because most prawns exhibit this pattern. Indeterminate growth continues indefinitely after the onset of sexual maturity until death. For the Crustacea, indeterminate growth strategies can be further divided into those that lay eggs during every post-sexual-maturity instar and those that lay eggs in some, but not all, instars after sexual maturity. Some taxa in each of these categories lay a single batch of eggs per instar and others lay more than one batch per instar (Hartnoll 1985).

As with many crustaceans, prawns support their incubating eggs beneath the abdomen using pleopods, modified locomotor appendages. In female prawns, the onset of maturity is marked by a change in the setation of the pleopods (Green 1961; Hartnoll 1985) and in some species, the ovigerous setae are present only during the breeding season (Green 1961). The change in the pleopod setation in prawns is generally followed by indeterminate growth. Prawns mate shortly after the female has moulted. One batch of eggs is laid per instar, but not all instars after sexual maturity are ovigerous. In most prawns, there is a definite breeding season during which several instars are ovigerous. The breeding season is followed by a non-breeding season (Hartnoll 1985).

Typically, Crustacea begin post-embryonic stages as free-swimming larva or nauplii. However, the developmental stage at which the embryo hatches will depend on the reproductive strategy of that species. In some taxa, the incubation is so prolonged that the eggs may even hatch at the zoea or post-larval stage (Waterman & Chace 1960). After hatching, the young crustacean typically does not resemble the adult and undergoes a series of developmental moults, changing its structure from instar to instar (Meglitsch 1972). Generally, these crustacean larvae are pelagic filter predatory feeders (Waterman & Chace 1960).

Most Crustacea disperse in one of two main ways: the animal may be passively transported to other habitats, as when larvae are carried by a strong ocean

current; or the species may disperse using its own locomotor activity, as in the extensive migrations of adult crabs and prawns (Green 1961). Their dispersal is highly effective: prawns are ubiquitous in almost all aquatic environments. Their cosmopolitan distribution includes intertidal to deep ocean waters, and from freshwater to highly saline environments (Green 1961; Meglitsch 1972). In particular, prawns of the family Palaemonidea occur world-wide in a wide range of habitats, including freshwater, brackish water, and marine environments (Kirkpatrick 1981; Kirkpatrick & Jones 1985; Corey & Reid 1991). However, regardless of the type of dispersal, the strategy adopted by a particular organism determines its success in reaching appropriate environments for breeding and refuge, and extending its range. To survive, animals generally must use behavioural and life history strategies suited to the new environmental conditions encountered (McLusky 1971; Meglitsch 1972; Stearns 1976). Within their area of distribution, many prawns, including some species of *Palaemon*, migrate to deeper waters during winter and return in spring to shallower waters for reproduction (Guerao & Ribera 2000). These migrations, in addition to the wider passive dispersal of individuals, probably promote that dispersal by exposing different life history stages to opportunities of moving, or being moved, longer distances. Seasonal migrations have been suggested for *Palaemon affinis* (Kirkpatrick 1981; Jones 1983) but there is no published evidence of prawns from deeper habitats to support such migrations. Whether or not *P. affinis* migrates to deeper waters and back, its estuarine and rock pool habitats would allow wide dispersal of both the nauplii and adults; supporting its wide distribution in different habitats throughout New Zealand (Morton and Miller 1968).

Life history and behavioural strategies are also influenced by the interactions within the community even when in a suitable physical environment. These interactions are highly complex and constantly changing. In terms of evolutionary theory, environmental factors influence adaptations and as one adaptation, or trait, changes as a result of selection pressure, the definition of the environment is changing as well. Traits also co-evolve, as one trait changes, other traits also undergo compulsory or opportunistic changes that together lead to a highly complex, continually evolving community structure (Stearns 1976). The structure is further complicated by the presence of many other species in the community.

Competition and predation are key environmental factors determining the type of life history strategy and behavioural adaptations used by species in all major taxonomic groups. The effects of competition and specialisation in food choice can be seen in the different structural and behavioural strategies developed by crabs in relation to food resources (Seed & Hughes 1995). Seed & Hughes (1995) found claw morphology reflected the type of handling techniques and foraging behaviour of crabs. Crabs that depend on rapid moving prey had faster weaker-acting claws, while crabs that preyed on hard-shelled molluscs had at least one larger, more powerful claw for crushing the shell. Some crabs had dimorphic claws with one crushing claw and the other smaller and less robust for capturing and manipulating the prey and for tearing and cutting the flesh. In addition, Seed & Hughes (1995) suggested counter adaptations by prey to avoid predation, illustrated, for example, by the shell morphology. Many molluscs have developed thicker shells, spines, or narrow or toothed opercular openings to avoid predation (Seed & Hughes 1995). The strategy used by any species will evolve in response to the selection pressures imposed by the physical environment as well as those resulting from interactions in the community. Its adaptation to the interactions allows it to survive in that community.

Successful structural adaptations and life-history strategies must be associated with the evolution of appropriate behavioural patterns. Crustacea have rich behavioural repertoires for locomotion, reproduction and feeding (Green 1961); the appearance of a particular behaviour is influenced by a wide range of environmental factors (Waterman & Chace 1960), including rhythmic changes in the environment induced by the sun or moon (diel and circatidal rhythms) (Green 1961; Rodriguez & Naylor 1972; Fincham & Furlong 1984; Guerao 1995; Guerao & Ribera 1996). Cyclic changes in the environment, such as temperature, are primarily induced by the sun, but tidal cycles, possibly the most important variable in marine intertidal environments, are caused primarily by the moon. Different behavioural patterns may be exhibited at different stages of the tidal cycles. For example, many intertidal species increase their activity on the rising tide. A rising tide usually allows a species to extend its foraging area to areas that were not submersed at low tide (McDowall 1969; Palmer 1995).

An animal may exhibit either exogenous or endogenous rhythms. An exogenous rhythm is a direct response to an environmental change that does not continue under constant conditions. An endogenous rhythm is innate and continues under constant conditions (Hardy 1969; Palmer 1995). Endogenous rhythms also referred to as "biological clocks", govern the periodicity of behaviours and physiological functions that occur on longer time scales. For example, Guerao & Ribera (1996) found the locomotor-activity of *Palaemon serratus* showed an endogenous diel rhythm. The prawn's maximum locomotor activity occurred during times of expected night when held under constant infrared light for 3 days. Guerao & Ribera (1996) suggest the use of endogenous diel patterns may reduce the prawn's risk of predation. Regardless of the type of rhythm used by a species, the behavioural patterns are influenced by environmental factors and only those species using behavioural patterns appropriate to their environment will survive in that habitat.

The combination of life history strategies and behavioural patterns of a species in relation to the demands of its environment will determine the success of its long-term survival (Stearns 1976). *Palaemon affinis* occurs in intertidal habitats, which are constantly subjected to extreme environmental fluctuations, most especially to changing salinity and temperature (Morton & Miller 1968). The type of strategy used by *P. affinis* is not only influenced by these changing environmental factors, but also by the interactions within the community, such as competition and predator avoidance. To understand how successful *P. affinis* will be in surviving in future generations, a basic knowledge of its life history strategies and behavioural patterns is essential. Additionally, *P. affinis* is one of the largest and most abundant species in New Zealand intertidal habitats (Yaldwyn 1954; Richardson & Yaldwyn 1958; Morton & Miller 1968; Kirkpatrick 1981; Kirkpatrick & Jones 1985) and may potentially be useful in determining the health and stability of these communities. The aim of this thesis is to present a basic introduction to key biological adaptations of *P. affinis* in relation to its community, food preferences and behavioural patterns.

1.2. Study species

Palaemon affinis Milne-Edwards, 1837 (Plate 1.1) is the commonest prawn in intertidal habitats of the North and South Islands of New Zealand. The distribution of this endemic species includes rock pools, estuaries, and mangrove swamps (Yaldwyn 1954; Richardson & Yaldwyn 1958; Morton & Miller 1968; Kirkpatrick 1981; Kirkpatrick & Jones 1985). In the past, *P. affinis* was reported to have a southern circumpolar distribution until Holthuis (1952) discovered the species responsible in the western Atlantic, from Uruguay to the West Indies, was not *P. affinis*, but *Palaemon northropi* Rankin, 1898. Holthuis later restricted the distribution of *P. affinis* to New Zealand (Yaldwyn 1954).

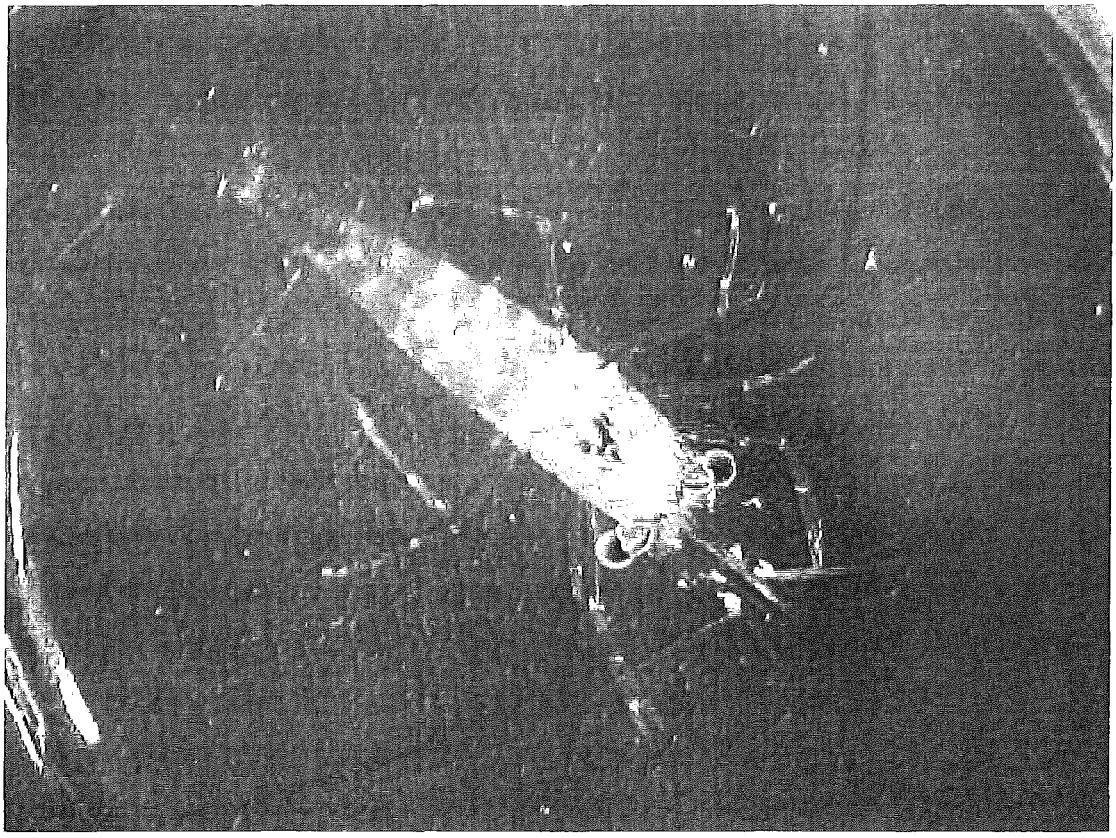


Plate 1.1 Adult *Palaemon affinis* Milne-Edwards, 1837 from Point Kean, Kaikoura.

Despite *P. affinis* being a common and conspicuous species in New Zealand, little has been published on its biology. Most contributions have focused either on morphological accounts of single individuals or the physiology of the animal. There

are no published descriptions on the growth patterns of *P. affinis*. Yaldwyn (1954) gave an extensive morphological description of the species including measurements of a male and female prawn, but did not give population data. According to Yaldwyn (1954), a male prawn had a carapace length of 6.1 mm and a total body length of 36.0 mm, whereas a female prawn had a carapace length of 13.3 mm and a total body length of 57.2 mm. He did not record weight or the parameters of the length measurements. In addition, no size ranges for either male or female was presented. However, the maximum length of the prawn, either sex, was later reported as ~75 mm by Richardson & Yaldwyn (1958).

Kirkpatrick (1981) presented some preliminary data on size ranges for *P. affinis* from a population from McCormacks Bay in the Avon-Heathcote Estuary. However, her research was focused on salinity tolerance and osmoregulation of the prawn, so her data are inadequate for investigating biological aspects, such as growth patterns. Kirkpatrick (1981) also presented linear equations for the relationship between the total body length and carapace length of male and female *P. affinis*; for females, Y (the total body length) = -0.012 + 2.071 X (the carapace length), $r = 0.995$, and for males, Y = 0.434 + 1.818 X, $r = 0.906$. However, the relationships were not supported by data or literature citation so the validity of neither can be confirmed.

Little has also been published about the reproductive biology of *P. affinis*. Data on reproduction is limited to the breeding period and the length of ovigerous female. Ovigerous females have been reported in September to March (Yaldwyn 1954; Richardson & Yaldwyn 1958; Morton & Miller 1968; Kirkpatrick 1981; Kirkpatrick & Jones 1985) with the smallest ovigerous female being 7.8 mm carapace length (Yaldwyn 1954). However, the site of collection of these females was not given, and the breeding period and size may vary between populations. The only reproductive data for a known population was given by Kirkpatrick (1981), but her data were limited to the length of ovigerous females, 15-21 mm carapace length. There is no published literature on the relationship between female size and the size of the egg mass. Data, including the weight and length of the ovigerous female, as well as the number and weight of her eggs, are essential for determining reproductive strategies.

The life history strategy of *P. affinis* will be influenced by the demands of its environment; hence, the type of strategy used by the prawn will determine its distribution. As noted, *P. affinis* occurs in a variety of intertidal habitats throughout New Zealand (Yaldwyn 1954; Richardson & Yaldwyn 1958; Morton & Miller 1968; Kirkpatrick 1981; Kirkpatrick & Jones 1985), and has even been reported as being "common in the brackish reaches of the estuaries" (Morton & Miller 1968, p. 540). However, the published literature on the distribution of *P. affinis* is limited to general description with no data presented to confirm the distribution and abundance of any given population. For example, Kirkpatrick (1981) noted that *P. affinis* occurred in McCormacks Bay and was found most abundantly amongst the rocks and concrete overhangs. She reported the abundance of prawns amongst the rocks to fluctuate, with the highest numbers occurring during high tide, night-time and summer months. However, Kirkpatrick (1981) did not present supporting data on prawn numbers in relation to these environmental variables. To determine an accurate account of the distribution and seasonal patterns of *P. affinis*, a more detailed study is needed which focuses on the abundance of prawns from a given population in relation to the changing environmental factors over an extended period.

Furthermore, to fully understand the life history strategy of *P. affinis*, the type of community in which the prawn occurs must be taken into account, along with the interactions between *P. affinis* and the fauna within the community. The interactions are further influenced by the behaviour of the prawn. To date, the *P. affinis* community has not been described and interactions within the community are unknown. Additionally, no description of *P. affinis* behavioural patterns has been presented. A first step to understanding the behavioural patterns of *P. affinis* would include laboratory studies on the behavioural repertoire of the species, alone, during interactions with others of the same species, its locomotion in still and moving water, behaviour with respect to shelter, and in its dealing with potential predators and potential prey. That background would define the possible, when examining an alternative hypothesis to its behaviour in the wild, where observations are much more difficult.

1.3. Research aims

The aim of this thesis is to describe the life history strategies of *Palaemon affinis* Milne-Edwards, 1837 in relation to the demands of its environment. The data presented will focus on the population dynamics of the species, the community or communities of which it is part, and the natural food preferences of *P. affinis* from three intertidal habitats from the South Island. In addition, some general behavioural patterns of prawns collected from the Kaikoura study site will be described. The research programme was as follows:

- Population dynamics, focusing on the distribution, growth patterns, and reproductive strategies of *P. affinis* from three known habitats.
- The *P. affinis* community composition in relation to seasonal changes and environmental factors.
- Natural food preferences of different size classes of male and female *P. affinis* over a year.
- Effects of tidal and light cycles on locomotor and feeding activity of *P. affinis*.

Chapter Two

Population Dynamics of *Palaemon affinis*

Chapter Two: Population Dynamics of *Palaemon affinis*

2.1. Introduction

The population dynamics of the prawn *Palaemon affinis* have not been described before. The data presented here introduces the distribution, growth patterns, and general reproductive strategies of the prawn at three sites in the north-eastern South Island. Growth and reproduction are fundamental aspects of the life history strategy of a species (Llodra *et al.* 2000). The life history strategy adopted by *P. affinis*, as with any species, determines its success in surviving in particular habitats; therefore, its life history strategy will at least in part determine its distribution.

The distribution of hyperbenthic organisms in tidal habitats can vary dramatically with the season and tidal cycles as the depth of the water column alters, and different substrate are exposed or immersed (McLusky 1971). Because of the difficulty in assigning absolute limits to the distribution of aquatic animals, the distribution of Crustacea is commonly expressed as the number of individuals collected from a particular population at a given time over an extended period of at least a year. This description was also appropriate for *P. affinis* because of the variety of habitats in which it has been found, and the possible seasonal and tidal movement of populations, especially those in the Estuary. Kirkpatrick (1981) presented some preliminary information on the distribution of *P. affinis* from McCormacks Bay in the Avon-Heathcote Estuary. According to Kirkpatrick (1981), *P. affinis* is found amongst the rocks in McCormacks Bay during high tide and its abundance there fluctuates seasonally and through each tidal cycle. Kirkpatrick suggested that the lower number of prawns present at low tide might be the result of the prawns entering deeper channels within the bay or being swept through the culvert drain during low tide. Lower abundance during winter might be attributed to migration of prawns to deeper water. Jones (1983) further suggested the prawns left the estuary with the out-flowing tide, to return again with the incoming tide. However, during my preliminary sampling, *P. affinis* was confined to only one part of the estuary, suggesting the distribution of the prawns may be more limited than suggested. To test for possible seasonal patterns at all three sites, the distribution of *P. affinis* was determined by the number of individuals collected bimonthly over a year. Data are presented for each

site to facilitate inter-population comparisons, which include the distribution and abundance of sexes, size classes, and fecundity, as well as for seasons.

When determining growth patterns in prawns, it is common to investigate the size of the prawn as well as its rate of growth. Growth rates, in this study, were determined by examining the relationships between various body size measurements (carapace length, CL, and total body length, TBL) and wet weight (W) using least square regressions. Growth patterns commonly vary between sexes in Crustacea, so morphometric relationships were determined for both sexes and comparisons were made to determine any sexual dimorphism with growth patterns. When comparing linear regression equations, differences between slopes are considered to be biologically more meaningful than differences between y-intercepts alone (Anger & Moreira 1998), so only differences between slopes will be described here.

Reproductive strategies in Crustacea are generally expressed in terms of fecundity (Anger & Moreira 1998). However, fecundity includes a wide range of aspects of reproductive effort, many of which require an in-depth study focused solely on reproductive biology. In this study, the reproductive potential of *P. affinis* was examined in terms of realised fecundity, a measure used elsewhere in studies on reproduction in other species of *Palaemon* (Emmerson 1985; Guerao *et al.* 1994; Anger & Moreira 1998). Realised fecundity is defined as the number of eggs carried beneath the abdomen of an ovigerous female (Anger & Moreira 1998), so relationships between fecundity and the size of ovigerous female were examined. In addition, the size at the onset of maturity in females was determined, to compare the reproductive strategy of different populations of *P. affinis*, as well as for interspecific comparisons with published literature.

2.2. Study sites

2.2.1. McCormacks Bay – Avon-Heathcote Estuary

McCormacks Bay forms the southern side of the equilateral triangle of the Avon-Heathcote Estuary (Fig. 2.1, 2.2). The Avon-Heathcote Estuary itself has an area of c. 8 km^2 with two spring-fed, slow flowing rivers entering at the northern (Avon River) and the western (Heathcote River) apices (Fig. 2.2). To the south, the Estuary is bounded by the Port Hills (the western end of Banks Peninsula); to the west

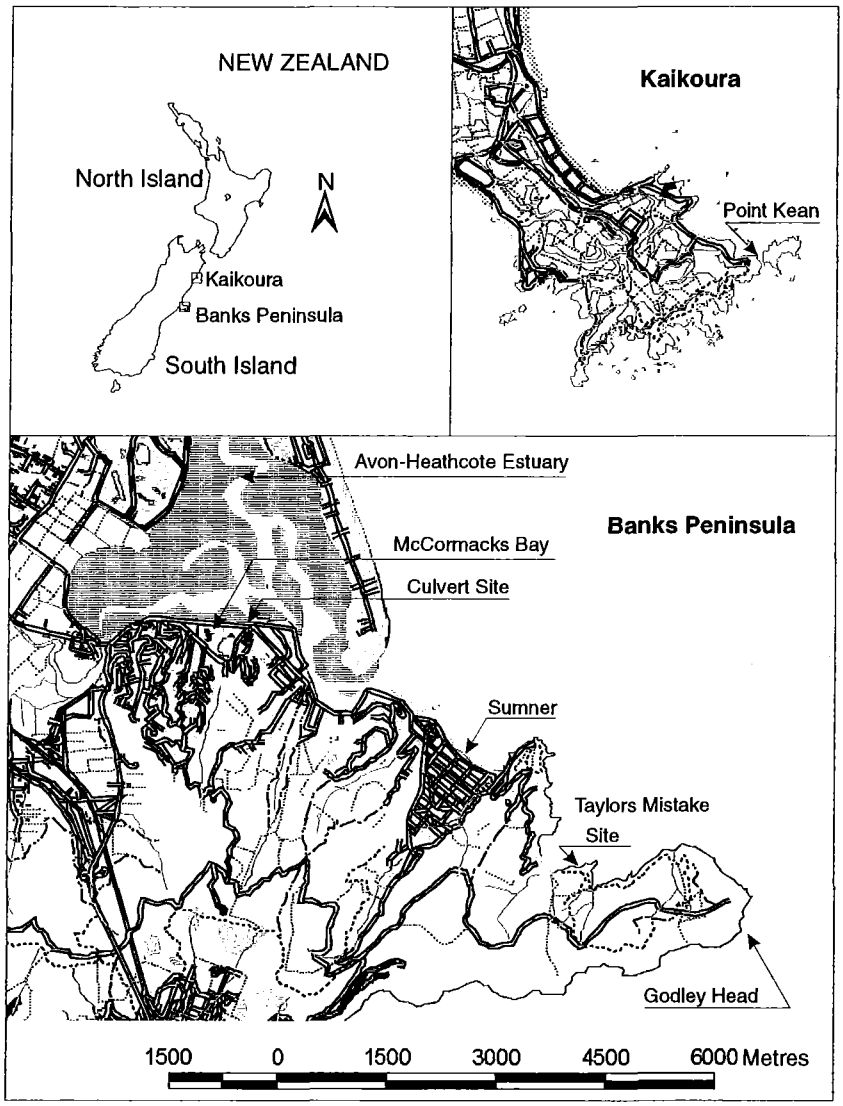


Fig. 2.1 Location map of study sites: the Culvert at McCormacks Bay, Taylors Mistake, and Kaikoura.

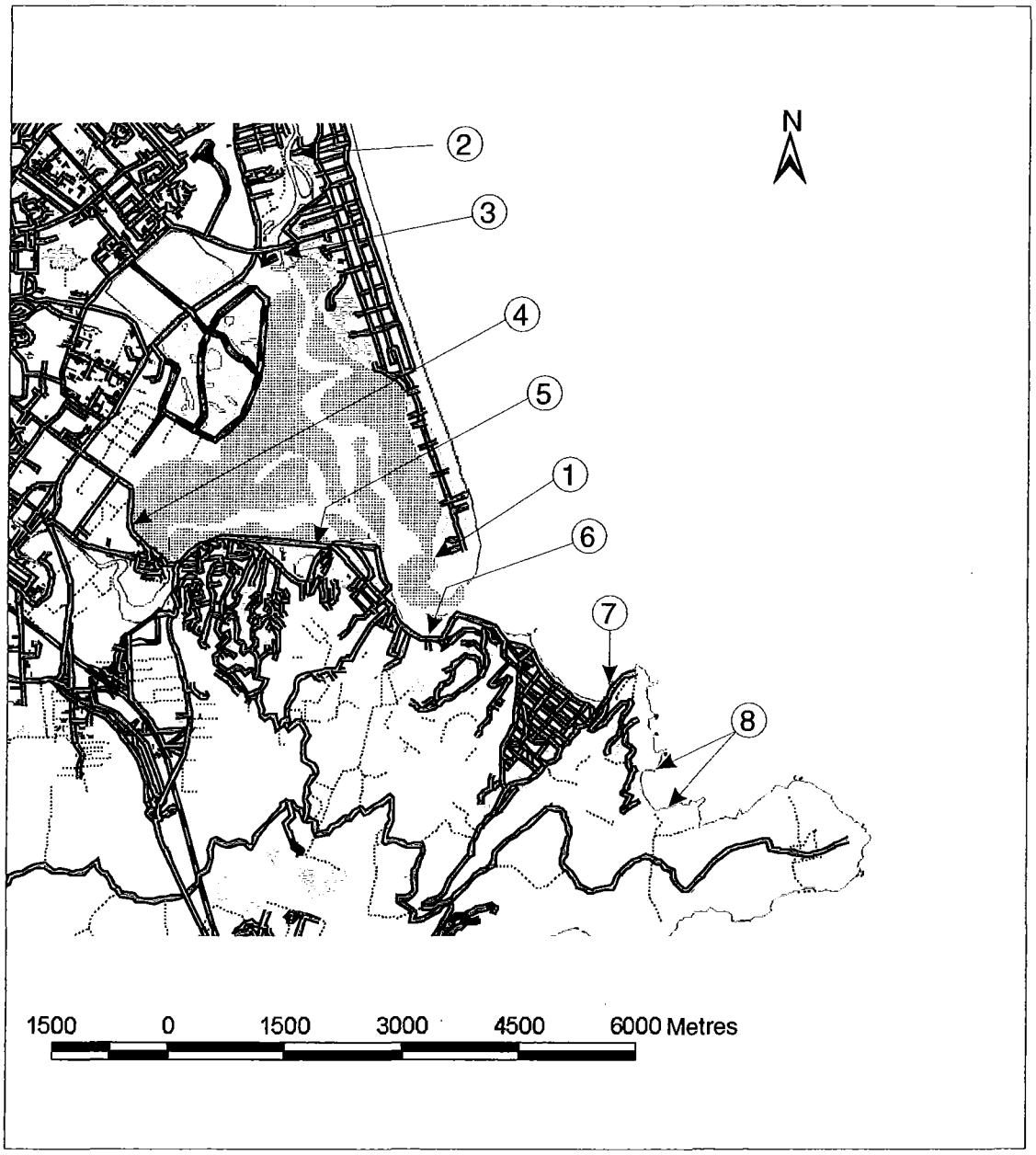


Fig. 2.2 Location map of preliminary sites at the Avon-Heathcote Estuary and Taylors Mistake. 1, Stilt Lane (South Brighton Spit); 2, Estuary Walk at Admiral's Way (Avon River channel); 3, Dyers Bridge (Avon River channel with intact marsh vegetation); 4, Humphreys Drive (upper estuary by a freshwater channel – Linwood Avenue Canal); 5, the eastern Culvert draining McCormacks Bay; 6, Moncks Bay (main channel near the entrance to the estuary); 7, Sumner Boat Club (main channel near the entrance to the estuary); 8, Taylors Mistake (rock pools east and west of beach).

by the city of Christchurch, and a water treatment facility; and Brighton Spit to the east (Knox 1969; Knox & Kilner 1973; Millward 1975; Owen 1992). The main sources of the sediments in the estuary are from the Port Hills whose basalt lavas are covered with ~20 m of loess, an easily erodible, silty, yellow sediment. Loess washed from the hills by heavy rains contributes to siltation of both the Heathcote River and the Estuary (Owen 1992).

McCormacks Bay lies at the entrance of a valley at the base of the Port Hills and is separated from the main body of the Estuary by a causeway and a stone and concrete wall (Fig. 2.1). The bay is divided into two parts, eastern and western, by another embankment and is drained by three culverts into the main body of the estuary. Two of the culverts, including the largest culvert that carries the bulk of the moving water, are in the western part of the bay. At low tide, the western area drains almost completely, except for a large pool at the base of the largest culvert. The eastern part of the bay is drained by a single culvert. Here, both the embankments which divide McCormacks Bay and separate the bay from the main body of the estuary act as dams, allowing the eastern part of the bay to retain a permanent water depth of 50-100 mm during low tide. The culverts carry strong turbulent flow (Knox & Kilner 1973; Kirkpatrick 1981). The rocks and fast flowing water of the bay support a fauna that is more similar to open water rocky shores than an estuary (Knox & Kilner 1973; Owen 1992). Adjacent to the causeway and McCormacks Bay, the main channels of the Heathcote River and Avon River merge near the mouth of the eastern culvert (Webb 1972; Knox & Kilner 1973). The site is c. 1.75 km from the mouth of the Estuary (Knox & Kilner 1973) along channels that are 0.8-7.3 m deep (Webb 1972). The substratum of these channels is mostly mud with cockleshell banks, with little to no algal beds.

The Culvert channel, stretching from the culvert drain to the main channel, was selected as a study site (Fig. 2.1 and Plate 2.1). The Culvert channel, which conveys water from the Bay at low tide, was c. 100 m long to its junction with the main channel with a maximum width of c. 8 m and 150-700 mm deep. The face of the embankment on both east and west sides of the culvert drain is composed of rock and rubble, which extends along the shoreline. The substratum of the Culvert channel was mostly mud with some small beds of cockle *Austrovenus stutchburyi*. There were

more rocks and shells in the bed near the mouth. Beds of algae, *Ulva lactuca* and *Gracilaria* sp., were common in the channel. Samples were taken just below the outlet pool of the culvert as preliminary investigations showed that prawn numbers were least at the culvert channel debouchment into the main channel.

Plate 2.1 McCormacks Bay, Avon-Heathcote Estuary site in February 2001. View west at the culvert channel draining the eastern part of McCormacks Bay into the main channel of the estuary at low tide. Culvert channel merges with the main low channel of the Heathcote River at lower right.

2.2.2. Taylors Mistake

Taylors Mistake Bay is c. 3 km east-southeast of the Avon-Heathcote Estuary, at the base of the northern side of Banks Peninsula (Figure 2.1). The small bay lies between Sumner and Godley Head, the western side of the entrance to Lyttelton Harbour. The bay itself has an unstable beach formed by deposits of dense basalt sand (Knox 1969) and is bounded by basalt cliffs to the east and west. The wave-cut platform at the base of the cliffs is covered with boulders, amongst which are rock pools of varying sizes. The surface of the basalt platform is c. 3 m above high water (McGregor 1964).

The rock pools at the base of the eastern cliff c. 200 m east of the beach were selected as a site (Fig. 2.1 and Plate 2.2).

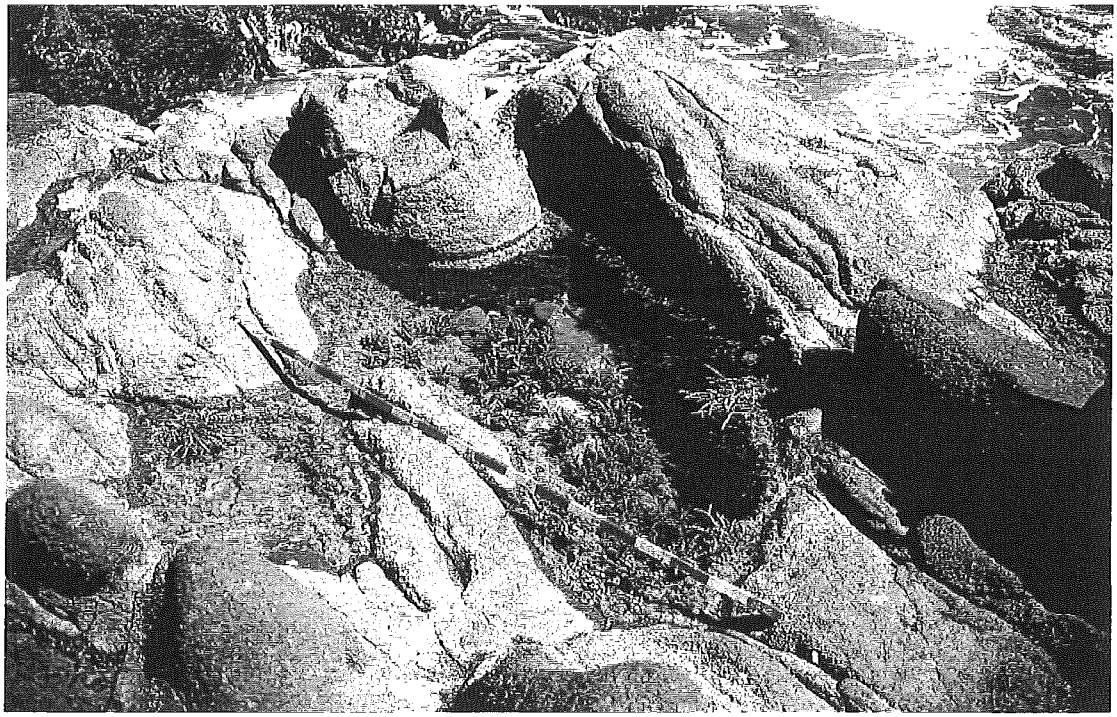


Plate 2.2 Taylors Mistake site in February 2001. View north over the largest study pool.

The rock pools, formed in rounded depressions and slots in the basalt platform, are subjected to strong wave action at high tide and during storms. The main algae in the rock pools were *Hormosira banksii* and *Corallina officinalis* turf. Because preliminary sampling showed that the abundance of *Palaemon affinis* fluctuated dramatically in any one pool at this site, three pools were sampled. The rock pools differed in size and depth: the largest was 1.5 x 1 m with a maximum water depth of 400 mm (Plate 2.2) and the smallest was 1 x 0.5 m, with a maximum water depth of 180 mm. Most prawns, especially the largest, were found in the largest pool amongst the algae and under rock overhangs. Because of the large sample size, data from the largest pool were used for analysis. Water depth at low tide was 50-400 mm.

2.2.3. Point Kean (seal colony), Kaikoura

Kaikoura Peninsula is 161 km north of Christchurch (McGregor 1964) and is the smallest and most northerly of three large peninsulas on the South Island's east coast (Fig. 2.1). The tip of the peninsula is narrow, about 1.2 km wide (McLay 1995), and is surrounded by a mudstone platform that is being lowered by erosion at about 1.5 mm/year (Kirk 1977). Kirk also recorded rates of erosion of up to 7 mm/year and lowering rates of 2-3% of the cliff retreat rates with 4000-5000 m^3 of rock being removed from the intertidal of the peninsula annually. Hence the platform is a dynamic setting on the longer time scale as well as during monthly tidal cycles. The platform extends intertidally for about 150 m northeast where it drops sharply to the sea floor (Marsden 1981; McLay 1995) and is frequently exposed to large ocean swells and storm waves (Woods & Schiel 1997).

Point Kean is at the eastern tip of the peninsula (Fig. 2.1). The rock platform there has many rock pools that are formed in the deeper cracks and crevices of the platform. Point Kean itself supports a large population of New Zealand fur seals (*Arctocephalus forsteri)*, which rest on the intertidal platform. The "seal colony" is a popular tourist attraction, not only for seal viewing but also for the diverse intertidal fauna. A car park has been built next to the platform. This car park is separated from the platform and sea, at some points, by a concrete sea wall. A rock pool c. 30 m east of the car park was selected as a study site because *P. affinis* was abundant there in the preliminary sampling (Plate 2.3).

Although the main body of the pool contained areas of *Hormosira banksii* and *Corallina officinalis* turf, a bed of *Zostera zealandica* bounded the southern sloping side. The northern edge was a vertical to overlapping wall of smooth rock. The pool was c. 2 x 5 m with a water depth of 50-300 mm. Larger prawns were found most commonly under the overhanging rock ledge and amongst the *Corallina* turf. Smaller prawns were typically found amongst the *Zostera*.

Other pools elsewhere on the platform were examined at times throughout the year. Prawns varied greatly in abundance in those pools, but the animals were found occasionally in pools higher or lower on shore than in the study pool. Prawns were found in other pools with a triangular hand-dipping net during winter months, but

were scarce in spring and autumn. They were never found in pools at low tide level or in small inlets below low tide level.

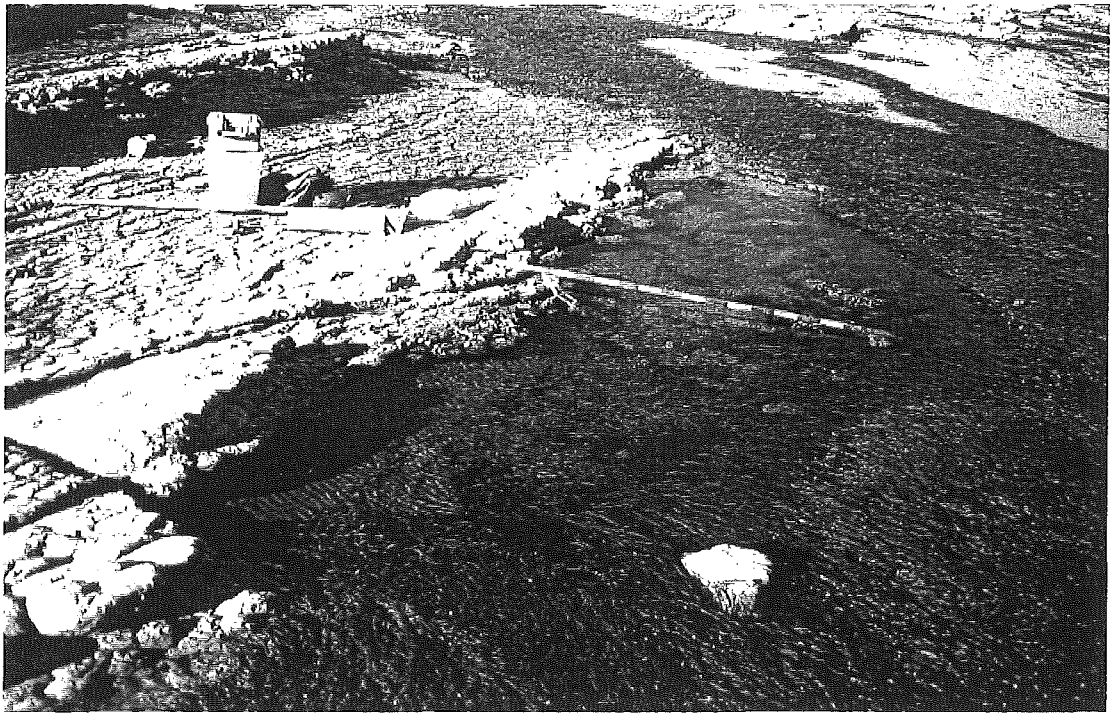


Plate 2.3 Kaikoura study site at Point Kean in February 2001. View east over study rock pool.

2.3. Methods

2.3.1. Site selection

2.3.1.1.Preliminary survey

In February 2000, I surveyed the distribution of *P. affinis* within the Estuary as a basis for selecting an intensive-study site. Eight preliminary sampling sites were chosen (Fig. 2.2), reflecting the geographical extent of the Estuary and the range of habitats available. The sites were Stilt Lane (South Brighton Spit), Estuary Walk at Admiral's Way (Avon River channel), Dyers Bridge (Avon channel, with intact marsh vegetation), Humphreys Drive (upper estuary by a freshwater channel – the Linwood Avenue canal), the eastern culvert draining McCormacks Bay (draining a major cut-off of the estuary and a known site for the species), Moncks Bay (main channel near the entrance to the estuary), Sumner Boat Club (main channel near the entrance to the estuary), and Taylors Mistake (rock pools near the entrance to the estuary). Six of the

sites were selected on the basis of records of prawn remains in fish guts from various localities in the Estuary (Webb 1973), or by their superficial similarity to the habitat in or near McCormacks Bay, such as the presence of beds of *Ulva* or *Gracilaria*, or possession of a rocky shoreline, as well as the geographic distribution around the estuary. The Taylors Mistake site was selected because of reports of *P. affinis* in rock pools there (Knox 1969; R. Bishop, personal communication).

Sampling was done by hand-pulling a 3.85 x 2.16 m (1 mm mesh) net, weighted by a chain along the lower edge and with floats at the top edge, extended between two people at low tide at the estuarine sites. A triangular hand-dipping net was used to capture prawns amongst the rocks and in rock pools that were at the base of the cliffs east of the beach at Taylors Mistake.

2.3.2. Collection of *Palaemon affinis* and hyperbenthic communities

The sampling method used for hyperbenthic species depends on local conditions, such as substratum and water depth, as well as the research topic. Various methods have been applied, including hand-held dipping nets, push nets, sledges, and suction samplers (Mees & Jones 1997). As the study sites had a diverse substrata, a suction sampler was built that allowed semi-quantitative collections from both the soft substrate in the estuary channel and the hard substrate, including rock crevices and overhangs, in rock pools.

The suction sampler was a cylindrical chamber fitted with a manual piston (Plate 2.4). The chamber was a PVC pipe with 102 mm internal diameter, 448 mm long. The piston was a 10 mm diameter, 637 mm long steel rod with steel crosspiece welded to the outer end. The piston was 23 mm thick, formed from a sandwich of two 4 mm PVC disks with 6 layers of dense felt material trimmed to 0.5-1 mm greater diameter than the internal diameter of the cylinder. Petroleum jelly (Vaseline®) was applied to the periphery of the piston before each sampling to provide an effective water/air seal for the piston within the chamber. The suction sampler sampled a surface area of 0.0082 m^2, and a volume of 0.3473 m^3 at full extension to a drain hole 400 mm from the suction.

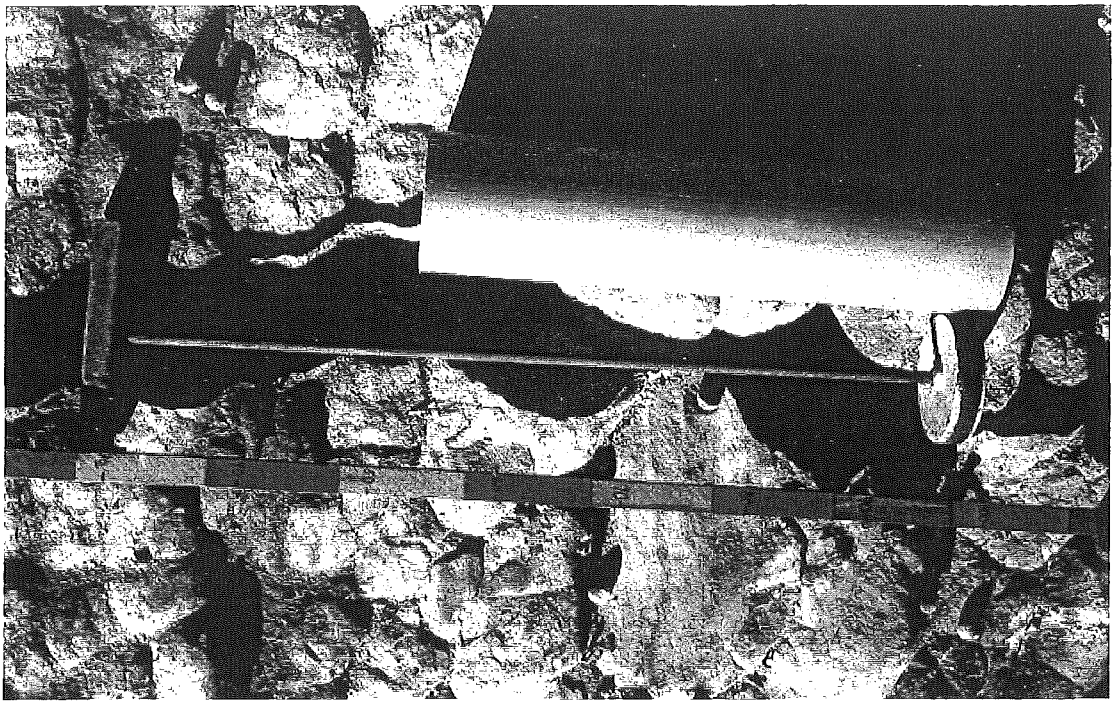


Plate 2.4 Suction sampler used for bimonthly sampling of the hyperbenthos at all three sites. Sampler consists of a cylindrical chamber (PVC pipe, 102 mm internal diameter, 448 mm long) fitted with a piston (10 mm diameter, 637 mm long steel rod with steel cross-piece welded to outer end and 23 mm thick sandwich of 2 mm PVC discs and 6 layers of dense felt), sampling a surface area of 0.0082 m^2, and a volume of 0.3473 m^3 at full extension.

For collection of *Palaemon affinis* and the hyperbenthic community, the chamber with the piston lowered was placed next to the substrate. The piston was pulled quickly, sucking a volume of water and some substrate into the chamber. The suction sampler could lift cockles from the sediment and algae not strongly attached to the substrate. While keeping the chamber mouth beneath the water surface, the contents were expelled into a 1 mm mesh sieve. Mees & Jones (1997) suggest that a 0.5-1 mm mesh is satisfactory for collecting hyperbenthic macrofauna. Five random suction samples were taken from each of the three sites during low tide, at two monthly intervals from February 2000 to January 2001. Prawn samples were preserved in the field in seawater to which 10% formalin was added.

Whenever possible, 20 prawns were collected during each sampling and preserved in individual containers for morphometric, reproductive, and gut content analysis. If more than 20 prawns were collected with the suction sampling, the extra number was recorded. The extra prawns were released when sampling was completed to avoid over-harvesting. If fewer than 20 prawns were collected during the suction sampling, that number was recorded and additional prawns up to the 20 required were caught using a hand-pulled trawling net in the estuary and a hand-dipped triangular net in the rock pools. However, because of changes in abundance and seasonal distribution of *P. affinis* at some sites, the full sample of 20 prawns could not always be collected for all sites. All samples were returned to the laboratory for analysis. *P. affinis* was measured, sexed, and dissected for stomach content analysis.

2.3.3. Measurements

2.3.3.1.Length

Total body length (TBL) is commonly used as a measurement of body-size in crustacean biology. However, the measurements have not always been standardised. While in some studies TBL has been measured from the rear margin of the orbit to the base of the median distal telson spine (e.g., Anger & Moreira 1998), others have measured from the tip of the rostrum to the posterior end of the telson (e.g., Guerao *et al.* 1994; Tamaki *et al.* 1997; Guerao & Ribera 2000). In this study, I measured from the tip of the rostrum to the posterior end of the telson. All measurements were taken to the nearest millimetre with the animal under a dissecting microscope (6.3x to 40x). Millimetre size classes were chosen because the angles at which the animal's surface presented to the plane of measurement did not allow repeatable measurements with greater precision.

Although carapace length (CL) is also commonly used as a measurement of body-size in prawns, the dimensions also appear not to have been standardised. In some studies (e.g., Anger & Moreira 1998; Primavera *et al.* 1998; Kuun *et al.* 1999), CL has been measured from the postorbital margin to the mid-dorsal posterior edge of the carapace, where as in others (e.g., Kirkpatrick 1981; Kirkpatrick & Jones 1985; Campbell & Jones 1989; Hartnoll & Salama 1992) the measurement has been taken from the tip of the rostrum to the mid-dorsal posterior edge of the carapace. I

measured CL from the tip of the rostrum to the mid-dorsal posterior edge of the carapace to allow for intra-specific comparisons with data from Kirkpatrick (1981) and Kirkpatrick & Jones (1985). As before, all measurements were taken to the nearest millimetre with the animal under a dissecting microscope (6.3x to 40x).

2.3.3.2.Weight

Body mass is commonly measured in crustacean biology as both wet weight (Guerao *et al.* 1994; Guerao & Ribera 2000; Llodra *et al.* 2000) or dry weight (Anger & Moreira 1998). Hartnoll & Salama (1992) found that there was little variation between dry and wet weight in relation to size (expressed as carapace length). Because of this and to avoid drying the animals in case of subsequent analysis, wet weight was used in this study. The wet weight of males, barren females and gravid females was measured on an enclosed balance (Mettler ® AE 200) to 0.001 g. Before weighing, prawns were blotted with a tissue to remove excess surface moisture. Extra care was taken during this procedure with gravid females to avoid loss of eggs. After a gravid female was weighed, the eggs were gently removed from beneath the abdomen with forceps and the egg mass weighed separately. Ten eggs were then separated from the mass and weighed. Total number of eggs was estimated by simple proportion. Additionally, eggs were separated into two developmental stages, eyed and non-eyed eggs, at this time.

2.3.4. Sex determination

Sex of Crustacea is usually discerned using external morphology. In many studies (e.g., Yaldwyn 1954; Kirkpatrick 1981; Guerao *et al.* 1994; Tamaki *et al.* 1997; Anger & Moreira 1998; Guerao & Ribera 2000), the presence of the appendix masculina on the second pleopod is used as the basis for identifying males. However, smaller (externally non-sexable) males are morphologically similar to females and may be erroneously counted as females. The minimum size at which individuals can be reliably sexed should be determined to avoid bias in the measurable sex ratio (Anger & Moreira 1998).

I determined the sex of prawns using external morphology. The second right pleopod of each individual was removed and examined under a dissecting microscope for the presence (male) or absence (female) of the appendix masculina. For smaller individuals, examination was done under a compound microscope (40x to 100x). Carapace length of all individuals was measured, and the minimum length of discernible males was taken as the minimum size for calculation of sex ratios.

2.3.5. Statistical analysis

Statistical analysis was done using software STATISTICA® or PRISM®. All data were tested for deviations from Gaussian normality with the Kolmogorov-Smirnov (KS) test before any statistical analysis.

Relationships between different measurements of body size (TBL & CL), wet weight (W), and fecundity (FEC) were described by least square regressions, with natural logarithmic transformations of dependent and independent variables if necessary. Correlation and regression coefficients were tested for significant deviations from zero using analysis of variance (ANOVA) and slopes derived for the different regression equations were tested using analysis of covariance (ANCOVA). If no difference was found between slopes, the intercepts of the Y-axis were examined by ANOVA.

2.4. Results

2.4.1. Distribution

2.4.1.1.Preliminary results

In February 2000 during low tides, *Palaemon affinis* was collected at only one of the seven preliminary sites within the Avon-Heathcote Estuary: the eastern culvert draining McCormacks Bay into the Estuary's main body (Fig. 2.2). The distribution of *P. affinis* varied within the Culvert channel: more prawns were caught near the culvert drain and fewest towards the main channel; none was caught at the junction with the main low channel of the Heathcote River or in the main low channel. It is not known whether *P. affinis* were present in the bay itself because it was not sampled. Additionally, no *P. affinis* were observed or caught amongst the rocks

directly east of the beach at Taylors Mistake during the preliminary sampling (Fig. 2.2). Rock pools to the west of the beach and further east of the beach were examined later. Only one *P. affinis* was collected from the rock pools to the west, but numbers suitable for repeated sampling were found in pools to the east (Fig. 2.2). Rock pools at Kaikoura were also examined (Fig. 2.1), and numbers adequate for repeated sampling were present.

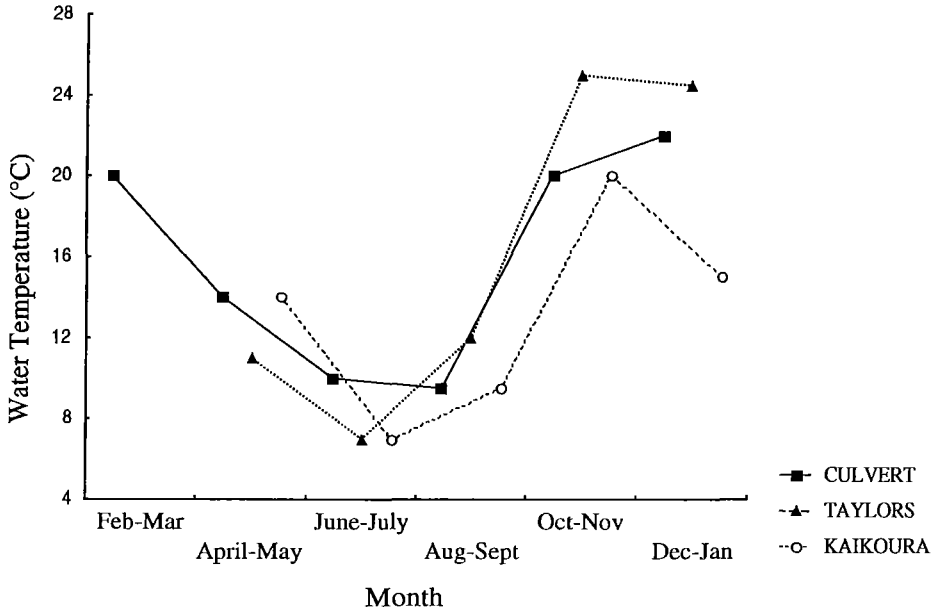
2.4.1.2.Environmental factors

Environmental factors within the three selected study sites (the Culvert channel, and rock pools at Taylors Mistake and Kaikoura) varied throughout the year. Water temperatures were lowest in winter and highest in spring and summer, whereas salinity was highest in winter and lowest in summer at all three sites (Fig. 2.3). For example, in the Culvert channel, water temperatures at low tide were lowest in winter (9.5°C in August), and highest in summer (22°C in December), while salinity was 35‰ in winter (June) and only 26‰ in summer (December).

Water depths also fluctuated during the year; for example, the minimum water depth at low tide at the Culvert varied between 10-30 mm, while the maximum water depth varied between 25-70 mm over the year. Water depth during the sampling was typically deeper within the Culvert channel than at Taylors Mistake and Kaikoura, but water depths also fluctuated within these sites over the year. Sampling was generally done during times of the first or third quarter moon, resulting in neap tides. However, the April-May and October-November sampling were done during a period of full moon and spring tides. Water depth measurements do not reflect differences in spring and neap tides. Measurements were taken during the time of sampling, not at dead low tide, so measurements appear to reflect the state of the tide at which it was sampled not the depth at low tide. However, other unknown variables may also be responsible for variations in water depth.

Storms effected the quality of the environment, especially at the rock pool sites. On June 4th and 5th a southerly storm occurred at Banks Peninsula. Sampling at Taylors Mistake was done on June 7th. Rock pools at Taylors Mistake were filled with lots of sand and broken shell, in addition to extremely cloudy water. No *Palaemon affinis* were collected from the pools at this time, but another prawn, *Alope*

a)



b)

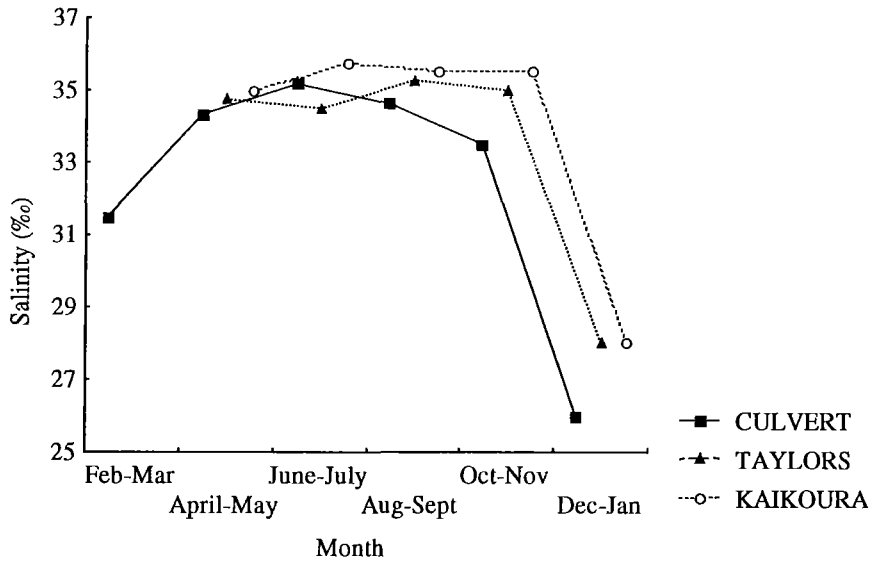


Fig. 2.3 Environmental variables from bimonthly sampling at the Culvert, Taylors Mistake, and Kaikoura in 2000: a, water temperature; and b, salinity.

spinifrons was found clinging to the undersides of rocks in the pools. Storms continued over the next week. Another sampling attempt was made on June 13th, but pools were inaccessible. The trail leading down the cliff was extremely muddy and slippery, and too dangerous to traverse. Pools to the west of the beach were examined instead. One *P. affinis* was found with a hand-dipped triangular net amongst *Corallina* turf, but no others were found. Pools to the west of the beach were filled with sand and broken shells, and water quality was poor. Conversely, abundant prawns were found at both the Culvert and Kaikoura during this time. Prawns were found in the majority of rock pools at Kaikoura in June-July, being most abundant in pools near-shore, and decreasing in abundance in pools closer to the sea.

As a side note, at Kaikoura, on August 12th the sampling pool was filled with lots of debris, most especially large pieces of bull kelp, *Durvillaea antarctica*, due to stormy weather. The debris was cleared away by the tides by the next day and pools were examined: *P. affinis* were found only in the sampling pool. Peak numbers were later recorded in the sampling pool just 3 days after the storm.

2.4.1.3.Seasonal patterns

P. affinis clearly changed in abundance seasonally (Fig. 2.4, 2.5). Similar patterns of abundance were found at the Culvert and Kaikoura sites, but the pattern was different at Taylors Mistake (Fig. 2.5). Low numbers of prawn, ≤175 individuals per m^2, were found at the Culvert and Kaikoura in autumn (April-May) and numbers dramatically increased to reach peak values (≥580 individuals per m^2) in winter (June-July). The population then declined dramatically to ≤125 individuals per m^2 in August-September and numbers remained low or absent throughout the spring and summer, October-January. When populations were peaking at the Culvert and Kaikoura in the winter, no *P. affinis* were collected by the suction sampler at Taylors Mistake. The Taylors Mistake *P. affinis* population peaked at 294 individuals per m^2 in April-May but it then declined suddenly to zero in June-July. By August-September the Taylors Mistake population was back to 171 individuals per m^2, but it declined again in October-January.

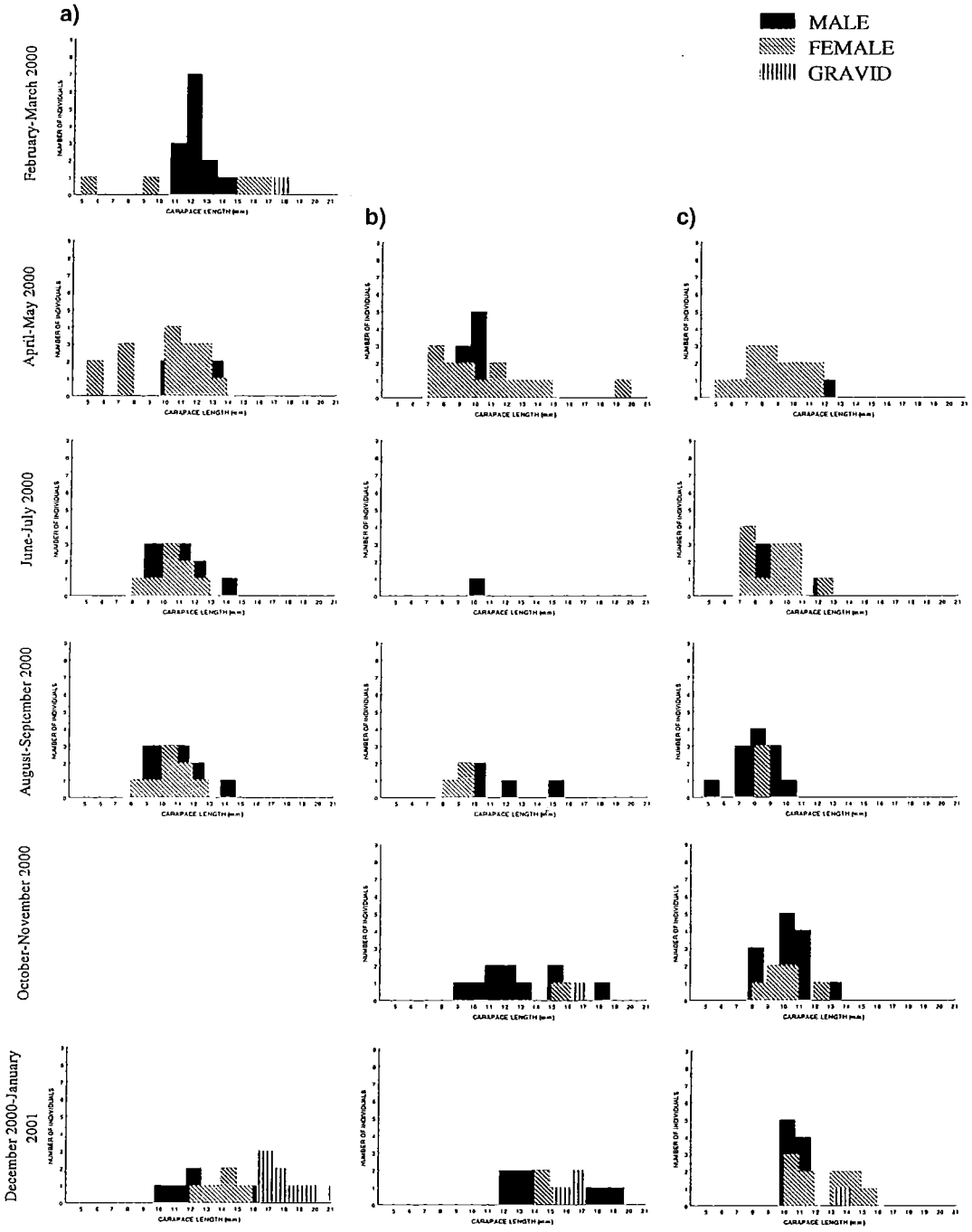
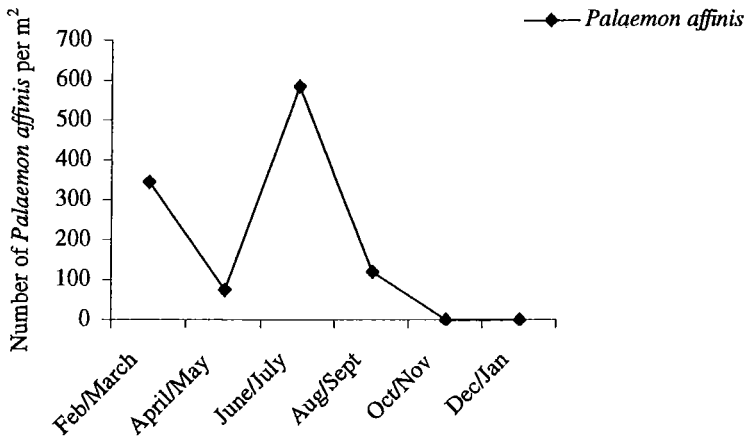
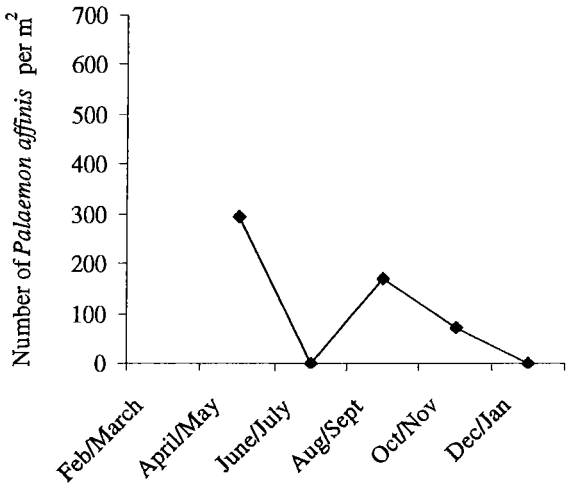


Fig. 2.4 Bimonthly distribution of male, barren female and gravid female *Palaemon affinis* in 2000 expressed as the number of individuals per carapace length (in mm units) from: a, the Culvert; b, Taylors Mistake; and c, Kaikoura. Data from up to 20 individuals collected by all sampling methods (suction sampler, hand trawled net, and triangular hand-dipping net).

a)



b)



c)

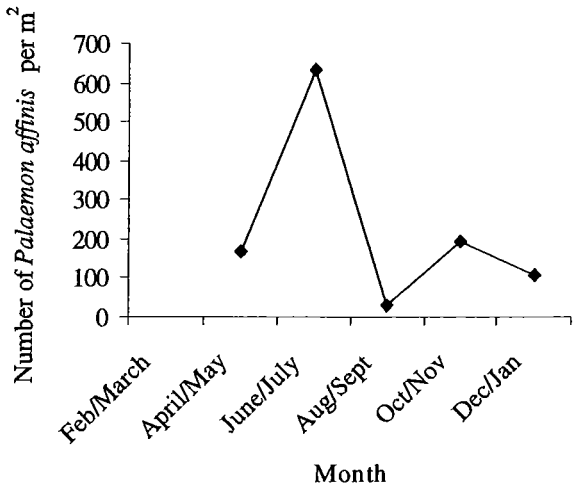


Fig. 2.5 Seasonal changes in *Palaemon affinis* abundance in 2000, based on bimonthly suction sampler sampling at: a, the Culvert; b, Taylors Mistake; and c, Kaikoura.

Prawns were not collected consistently by the suction sampler in any sites, except Kaikoura. No prawns were collected by the suction sampler from the Culvert from October to December (Fig. 2.5), although they were caught there in December by the hand-trawled net (Fig. 2.4). The net was not used in October (no net was available), so the presence of *P. affinis* at the Culvert site in October is based solely on specimens collected by the suction sampler. Similarly, at Taylors Mistake, no *P. affinis* were collected in June-July with the suction sampler, and only one was collected with the hand-dipping net at this time. This may be the result of the storm a few days before sampling. *P. affinis* apparently avoided the suction sampler in December at Taylors Mistake, but were collected there then in sufficient numbers for analysis with the hand-dipping net.

2.4.2. Sex ratios

Before discussing the results of growth and reproduction of *Palaemon affinis*, it is important to determine the size at which males could be identified morphologically (Minimum Externally Sexable Size, MESS) and the sex ratio of each population. The MESS of male *P. affinis*, determined by using the minimum value of carapace length, total body length, or wet weight, varied between all sites, ranging from 5 mm CL at Kaikoura to 9 mm CL at the Culvert (Table 2.1). All individuals collected from Kaikoura (n=100) could be sexed; some individuals below the 5 mm CL at Kaikoura may have been sexable, but none was collected. At the Culvert (n=9) and Taylors Mistake (n=3), some individuals were below the MESS and were excluded from the calculation of the sex ratio.

Using individuals ≥ 5 mm CL MESS, the sex ratio for the population at Kaikoura was 49 males: 51 females, with a MESS ≥ 8 mm CL for Taylors Mistake 13: 9, and with MESS ≥ 9 mm CL for the Culvert 47: 39 (Table 2.1). If individuals below the MESS were included in the calculation of population sex ratios, the standard sex ratio of 1 male: 1 female occurred at the Culvert and Kaikoura, while a 1.3: 1 ratio occurred at Taylors Mistake.

Conversely, when sex ratios were calculated for size class, skewed sex ratios occurred. Size class parameters varied between sites. At the Culvert, the small size class, 5-8 mm CL, was dominated by females (0 males: 9 females), medium size

Table 2.1 Range of carapace length (CL, mm), total body length (TBL, mm), and wet weight (W, g) of male and female *Palaemon affinis* collected from the Culvert, Taylors Mistake, and Kaikoura in 2000 and for pooled sites. M = males; F = females; *N* = number of observations; MESS = minimum externally sexable size of males; and *N* < MESS = number of observations of individuals < MESS.

	Culvert		Taylors Mistake		Kaikoura		Pooled Sites	
	M	F	M	F	M	F	M	F
N	47	48	39	30	49	51	135	129
CL (mm)	9-16	5-21	8-19	7-19	5-13	5-15	5-19	5-21
TBL (mm)	24-41	13-54	21-50	19-50	19-34	15-38	19-50	13-54
W (g)	0.107-0.553	0.021-1.729	0.084-1.091	0.060-1.310	0.060-0.397	0.028-0.513	0.060-1.091	0.021-1.691
MESS								
CL (mm)	9		8		5		5	
TBL (mm)	24		21		19		19	
W (g)	0.107		0.084		0.060		0.060	
N < MESS		9		3		0		0

class, 9-14 mm CL, by males (11: 6), and large, 15-21 mm CL, by females (1: 5). Size class parameters and sex ratio patterns were similar at Taylors Mistake; small size classes were dominated by females (2 males: 6 females), medium by males (29: 12) and large by females (8: 12). The female dominance of the small size class within both these populations may be inaccurate as individuals below the MESS of each population occur within this size class. The size class parameters at Kaikoura differed from the Culvert and Taylors Mistake, but similar sex ratio patterns occurred. The small size class, 5-8 mm CL, was dominated by females (7 males: 21 females), the medium class, 9-12 mm CL, by males (30: 23) and the large, 13-15 mm CL, by females (1: 6).

2.4.3. Growth

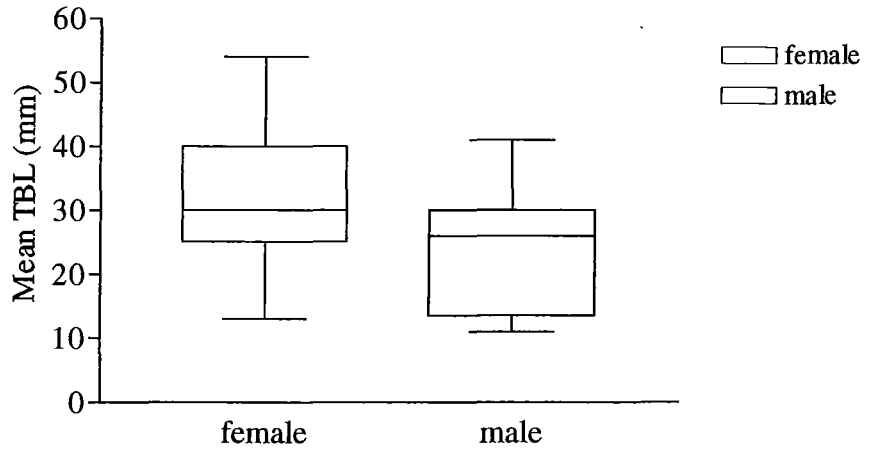
Significant correlations were found in all relationships between body size measurements (CL and TBL) and wet weight (W) of *Palaemon affinis* (Table 2.2). Differences in growth patterns were determined by comparing different linear regression equations, a significant difference between the slopes signified a difference in the rate of growth. Comparisons made between male and female wet weight excluded the wet weight of gravid females. Results of size and weight, as well as growth rates, of *P. affinis* are given for males and barren females within populations, between populations, and pooled data from all sites.

Within populations, male and barren female *P. affinis* differed in size and weight at the Culvert site alone (Fig 2.6a, 2.7a). Male prawns from the Culvert were significantly ($P<0.001$) smaller, when size was expressed as TBL, and weighed less ($P< 0.001$) than the females. The mean total body length and weight of males from the Culvert was only 23.8 ± 1.3 mm TBL and 0.258 ± 0.017 g, whereas the mean for the Culvert females was 32.2 ± 1.5 mm TBL and 0.424 ± 0.060 g. No sexual differences were found when size was expressed as carapace length (CL). Differences in size and weight of male and female prawns were not found at Taylors Mistake and Kaikoura, and may be the result of data not being collected for an entire year at these sites.

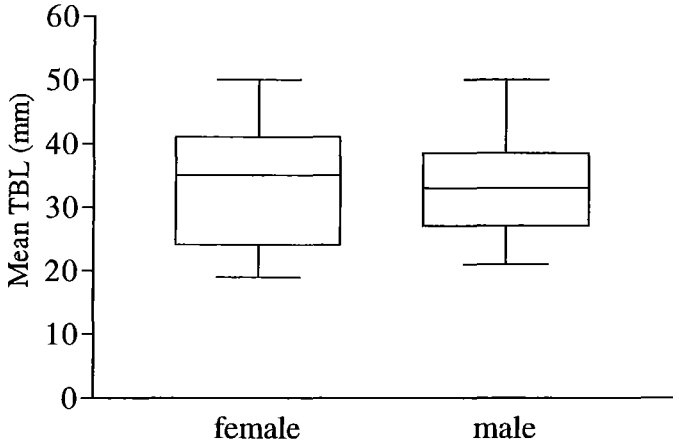
Table 2.2 Parameters of linear regressions (with or without natural logarithmic transformation of both X and Y values) describing the relationships between measurements of body size (mm) and wet weight (g) of *Palaemon affinis*. Data are given for males and barren females for comparison. TBL=total body length; CL=carapace length; W=wet weight; *N*=number of observations by data pairs; and r^2=coefficient of determination. Morphometric and size-weight relationships were calculated for males (M) and barren females (F) separately. Slopes were statistically compared between sexes with multiple ANCOVA; intercepts with ANOVA when slopes did not differ significantly. Significance is indicated with *, **, *** ($P<0.05$, $P<0.01$, $P<0.001$). When neither slope nor intercept were significantly different, regressions for pooled data, Σ, were given.

Y	*X*	*Sex/Stage*	*Intercept*	*Slope*	*N*	r^2
Culvert						
TBL	CL	Σ	1.9654	2.5191	86	0.9733
ln TBL	ln CL	Σ	1.1306	0.9428	86	0.9757
ln W	ln CL	M	-8.1180*	2.7462	47	0.9618
		F	-8.4272*	2.8954	39	0.9857
ln W	ln TBL	M	-11.3464***	2.8889	47	0.9801
		F	-11.8501***	3.0629	39	0.9895
Taylors Mistake						
TBL	CL	Σ	2.4578	2.4947	62	0.9402
ln TBL	ln CL	Σ	1.1522	0.9363	62	0.9531
ln W	ln CL	Σ	-7.9554	2.7308	62	0.9189
ln W	ln TBL	Σ	-11.0758	2.8466	62	0.9185
Kaikoura						
TBL	CL	Σ	2.8667	2.3886	99	0.9416
ln TBL	ln CL	M	1.4796	0.7845*	49	0.8671
		F	1.2163	0.8973*	50	0.9561
ln W	ln CL	M	-6.7719	2.1257**	49	0.7822
		F	-7.9798	2.6813**	50	0.9457
ln W	ln TBL	M	-10.9375**	2.7583	49	0.9348
		F	-11.5357**	2.9634	50	0.9729

a)



b)



c)

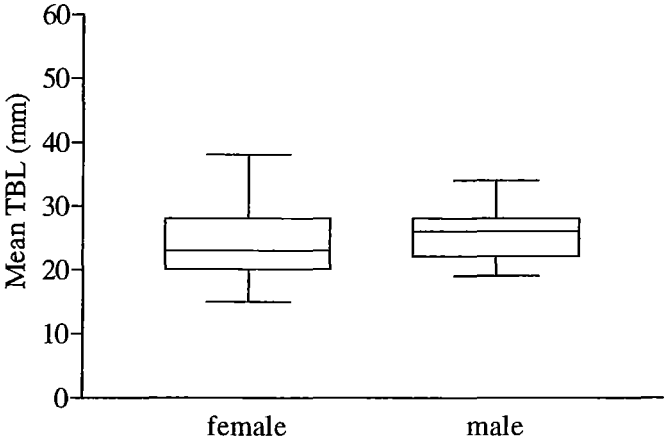


Fig. 2.6 Body size (mean total body length, TBL, mm) of male and barren female *Palaemon affinis* collected from three study sites in 2000: a, the Culvert; b, Taylors Mistake; and c, Kaikoura. Males and females differed significantly in length in the Culvert sample only ($P<0.001$).

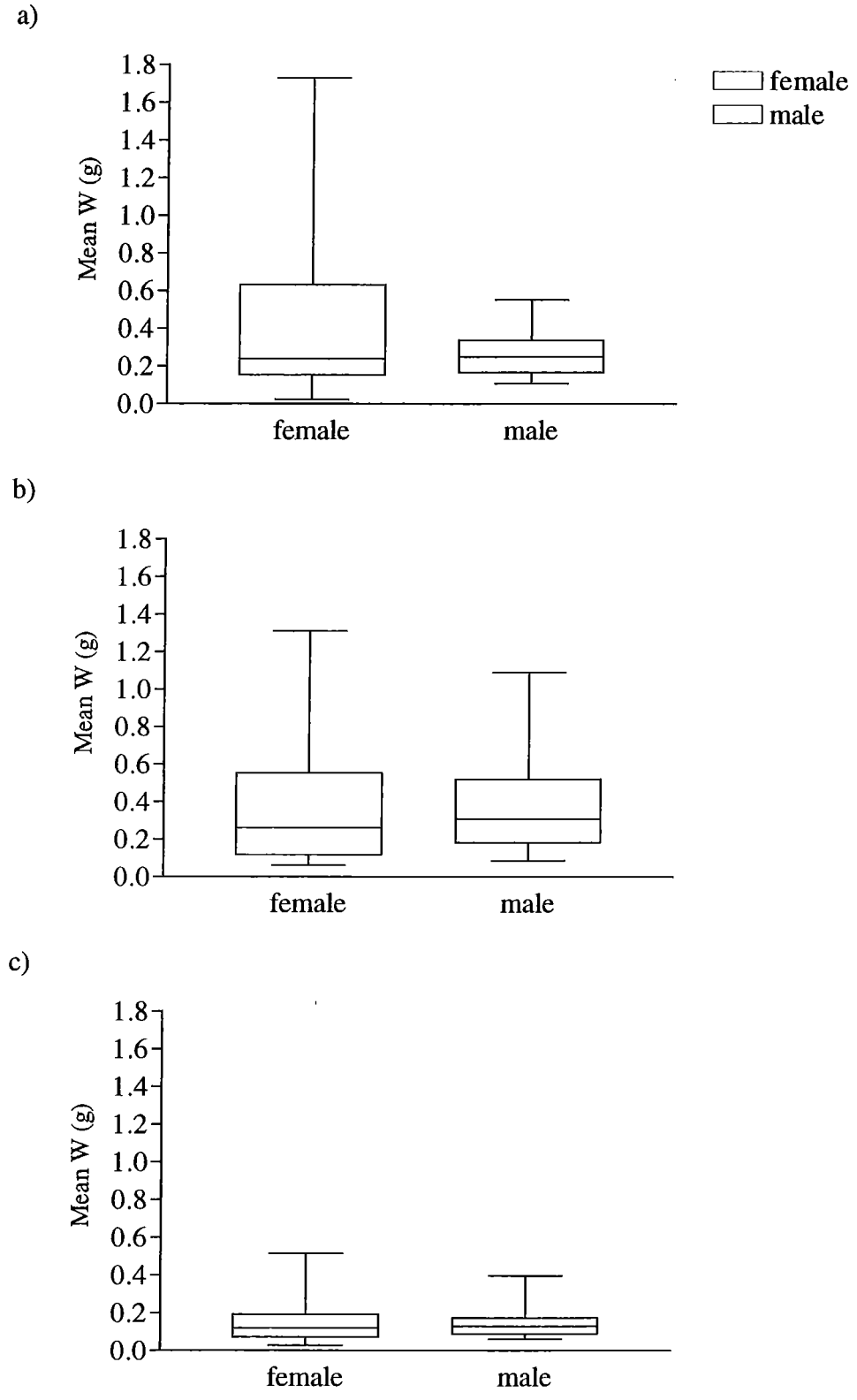


Fig. 2.7 Body mass (mean wet weight, W, g) of male and barren female *Palaemon affinis* collected in 2000 from: a, the Culvert; b, Taylors Mistake; and c, Kaikoura. Males and females differed significantly in body mass from the Culvert only ($P<0.001$).

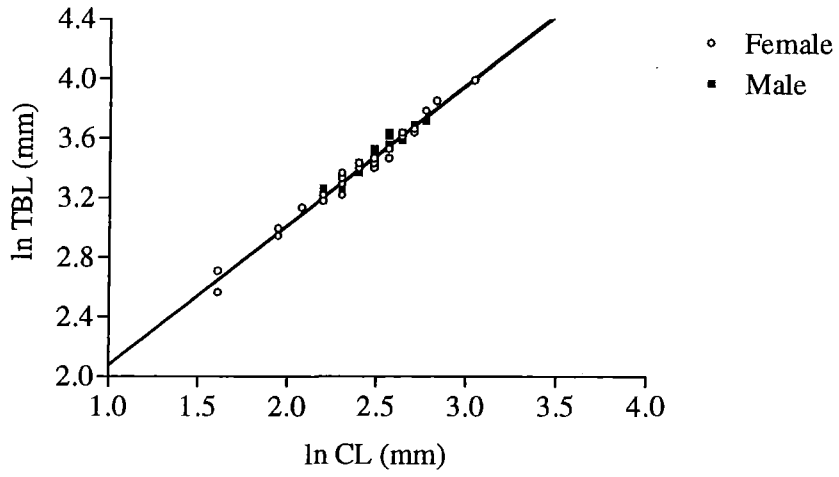
Differences in male and barren female growth rates were found at Kaikoura, but not at the Culvert and Taylors Mistake. When examining the relationship of lnTBL against lnCL of male and female *P. affinis* from Kaikoura (Fig. 2.8c), the females grew significantly ($P<0.05$) faster (slope≅0.9), than the males (slope≅0.8). A similar difference was found when examining lnW against lnCL; females grew significantly ($P<0.01$) faster (slope≅2.7) than the males (slope≅2.1) (Table 2.2). Difference in the growth rate of male and barren female lnW against lnTBL was not found.

Seasonal variation in size and weight occurred at the Culvert and Kaikoura, but not at Taylors Mistake. At the Culvert in February-March, males were significantly smaller ($P<0.001$), when size was expressed as TBL (Fig. 2.9a), and weighed less ($P=0.0287$) than the barren females (Fig. 2.10a). The mean total body length and weight of males from the Culvert was 12.5 ± 0.3 mm and 0.315 ± 0.021 g, whereas the mean for barren females was 35.5 ± 5.7 mm TBL, and 0.568 ± 0.173 g. In December-January, Culvert males were also significantly smaller (CL, $P=0.0078$: TBL, $P=0.0104$) and weighed less ($P=0.0089$) than the females (Fig. 2.9 a, 2.10a). The mean for males was 34.3 ± 1.9 mm TBL, and 0.335 ± 0.052 g, whereas the mean of barren females 42.3 ± 1.7 mm TBL, and 0.853 ± 0.122 g.

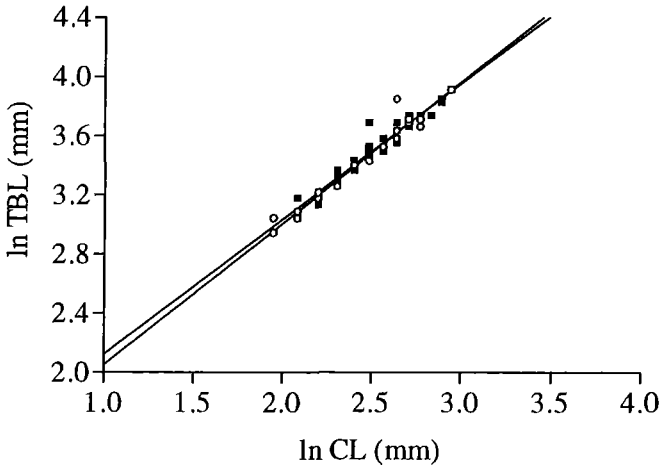
Seasonal patterns at Kaikoura were different from the Culvert, in August-September, males from Kaikoura were significantly larger ($P=0.0315$) (Fig. 2.9c) and heavier ($P=0.0057$) than the barren females (Fig. 2.10c). The mean for males from Kaikoura in August-September was 21.6 ± 0.6 mm TBL and 0.088 ± 0.060 g, whereas the females were 19.5 ±0.5 mm TBL and 0.063 ± 0.003 g. Conversely, in December-January, the females were significantly larger (CL, $P=0.0135$: TBL, $P=0.0063$) (Fig. 2.9c) and heavier ($P=0.0115$) (Fig. 2.10c) than the males. The mean for barren females at Kaikoura in December-January was 32.3 ± 1.2 mm TBL, and 0.295 ± 0.040 g, whereas the mean for males was only 27.9 ± 0.4 mm TBL, and 0.173 ± 0.008 g.

When comparing overall size and weight of *P. affinis* between populations, prawns from Kaikoura were significantly smaller and weighed less (CL, TBL, and W, $P<0.001$) than prawns from the Culvert and Taylors Mistake. Additionally, the total body length of prawns from Culvert were significantly smaller ($P<0.01$) than those

a)



b)



c)

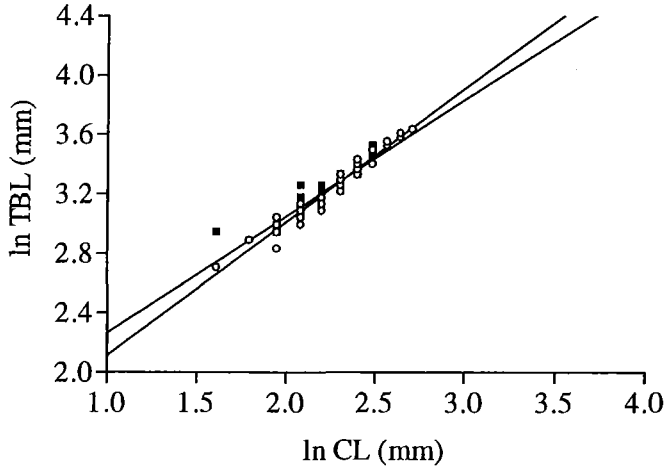
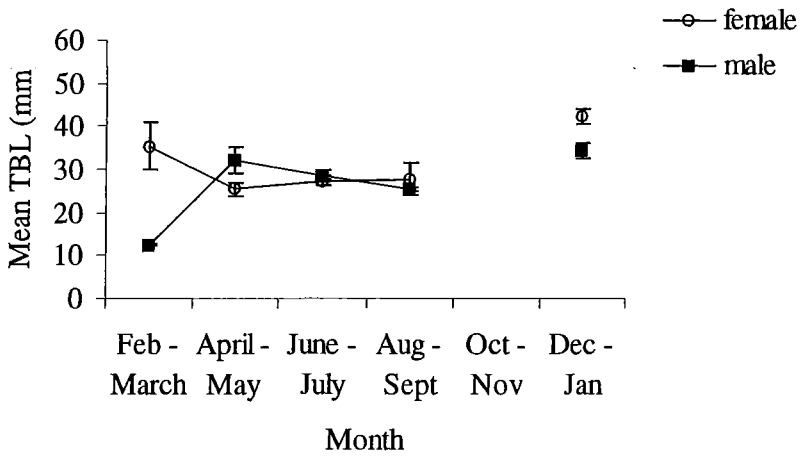
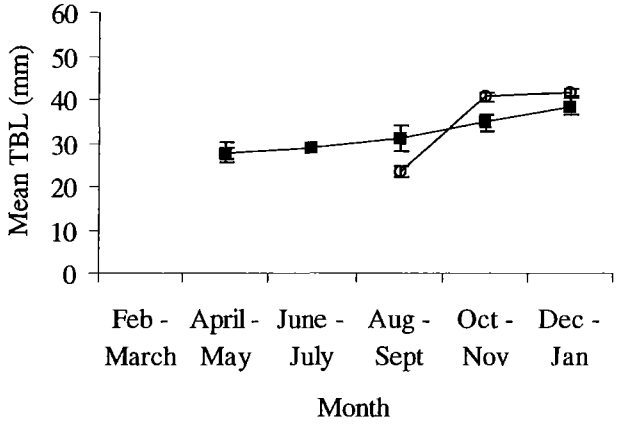


Fig. 2.8 Allometric relationship between carapace length (CL, mm, natural log transformed) and total body length (TBL, mm, natural log transformed) of male and barren female *Palaemon affinis* in samples collected from: a, the Culvert; b, Taylors Mistake; and c, Kaikoura in 2000.

a)



b)



c)

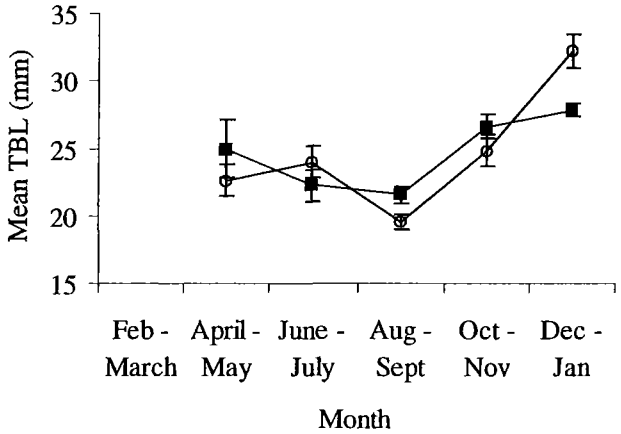
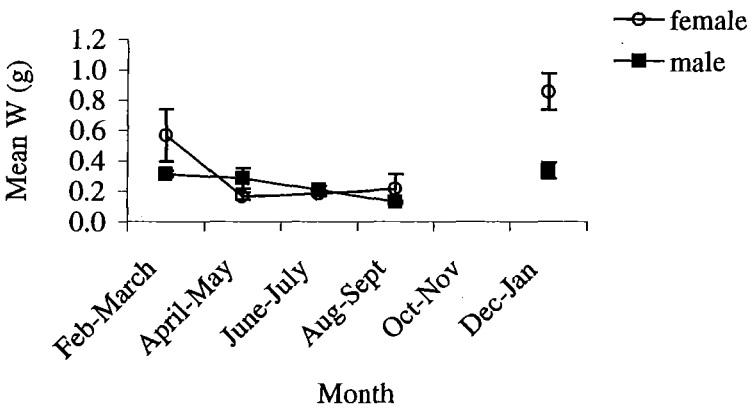
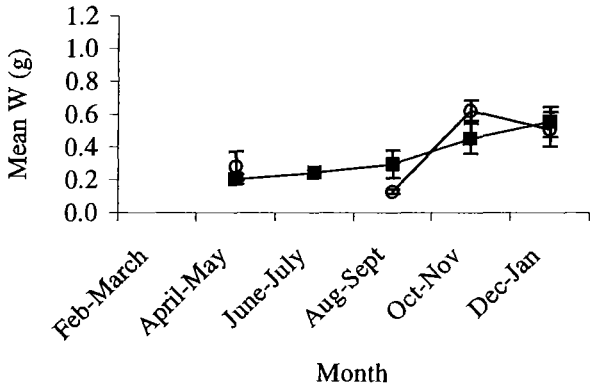


Fig. 2.9 Mean total body length (TBL, mm) of bimonthly samples of male and barren female *Palaemon affinis* collected in 2000 from: a, the Culvert; b, Taylors Mistake; and c, Kaikoura in 2000.

a)



b)



c)

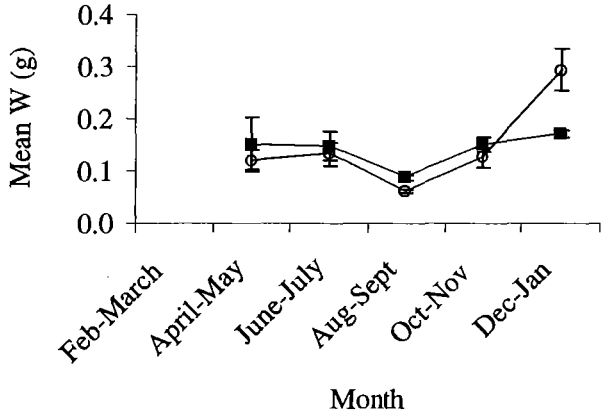


Fig. 2.10 Mean wet weight (g) of bimonthly samples of male and barren female *Palaemon affinis* collected from: a, the Culvert; b, Taylors Mistake; and c, Kaikoura in 2000.

from Taylors Mistake, but differences were not found between the CL and W. The mean total body length at Kaikoura was 25.3 ± 0.5 mm, at the Culvert, 28.1 ± 1.1 mm, and Taylors Mistake, 33.0 ± 1.0 mm.

Females differed in size and weight between populations. Females from Kaikoura were significantly smaller ($P<0.001$) than females from the Culvert and Taylors Mistake (Fig. 2.11). For example, the mean total body length of females from Kaikoura was only 24.8 ± 0.8 mm, whereas it was 32.2 ± 0.1 mm from the Culvert, and 33.3 ±1.7 mm from Taylors Mistake (Fig. 2.11b). Furthermore, the weight of females from Kaikoura differed significantly ($P<0.001$) from the females from the Culvert (Fig. 2.11c). The mean weight of females from Kaikoura was 0.150 ± 0.015 g, 0.331 ± 0.063 g at Taylors Mistake, and 0.424 ± 0.060 g at the Culvert. The size and weight of females from the Culvert and Taylors Mistake did not differ.

Patterns were not as clear-cut between the male populations. Males from Kaikoura were significantly smaller ($P<0.001$), when size was expressed as CL, than males from the Culvert and Taylors Mistake (Fig. 2.12a). The mean carapace length of males from Kaikoura was of 9.3 ± 0.2 mm, whereas the Culvert was 11.5 ± 0.3 mm, and Taylors Mistake, 12.1 ± 0.5 mm. This pattern did not persist when size was expressed as TBL (Fig. 2.12b). Males from Taylors Mistake were significantly larger ($P<0.001$) than males from the Culvert and Kaikoura, but differences were not found between the Culvert and Kaikoura. The mean male TBL from Taylors Mistake was 32.7 ± 1.2 mm, whereas Kaikoura was only 25.2 ± 0.5 mm, and the Culvert even smaller at 23.8 ± 1.3 mm.

The weight of males differed between all populations (Fig. 2.12c). Males from Taylors Mistake (0.371 ± 0.042 g) were significantly heavier than the Culvert (0.258 ± 0.017 g, $P<0.01$) and Kaikoura (0.139 ± 0.010 g, $P<0.001$), and the males from the Culvert were significantly heavier ($P<0.01$) than Kaikoura.

Differences in growth rates were found between males from the Kaikoura site and both the Culvert and Taylors Mistake sites, but not between the Culvert and Taylors Mistake (Table 2.3). When examining the relationship of lnW against lnCL, males from Kaikoura grew significantly slower (slope=2.1257) than males from the Culvert (slope=2.7462, $P<0.01$) and Taylors Mistake (slope=2.6483, $P<0.05$) (Table 2.3 and Fig. 2.13a).

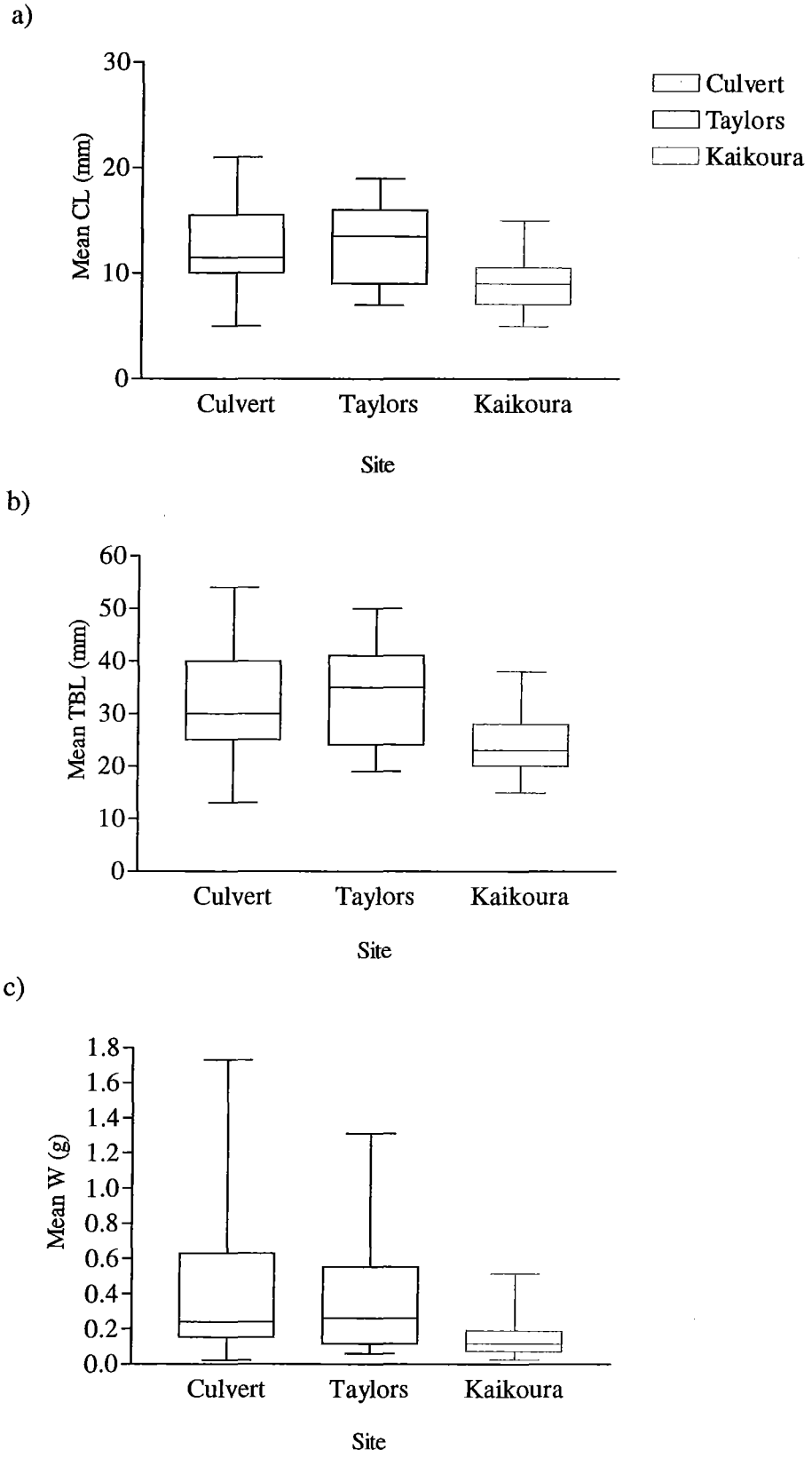
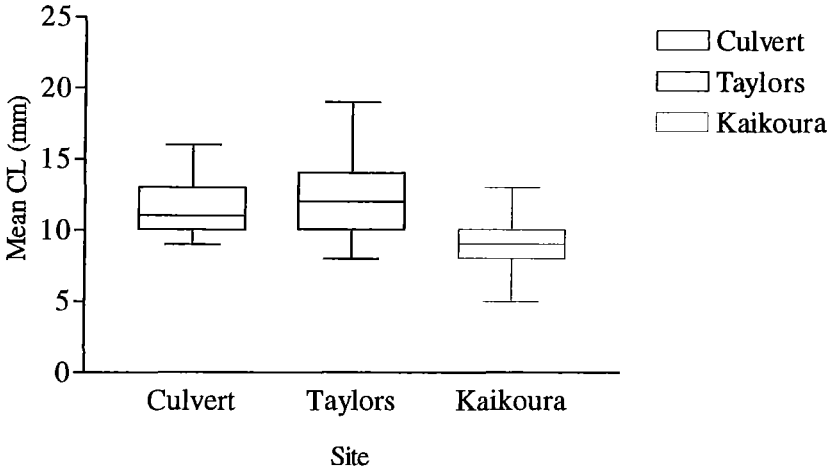
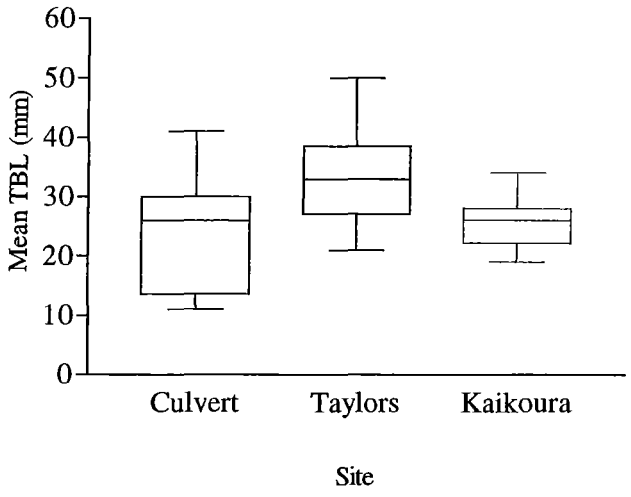


Fig. 2.11 Size of female *Palaemon affinis* collected from the Culvert, Taylors Mistake, and Kaikoura in 2000 as measured by: a, mean carapace length (CL, mm); b, mean total body length (TBL, mm); and c, mean wet weight (W, g).

a)



b)



c)

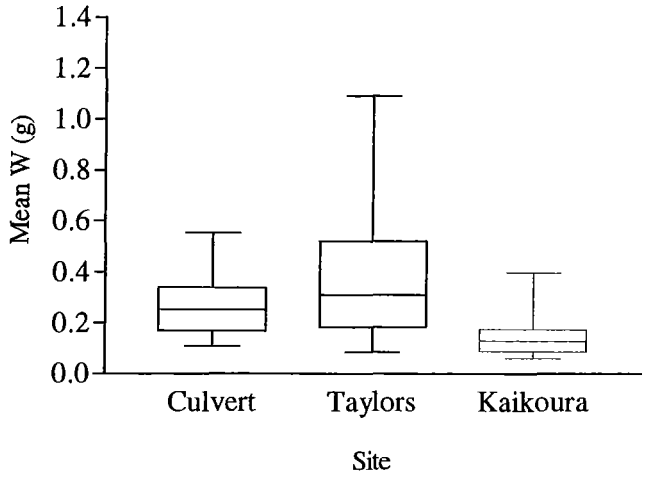
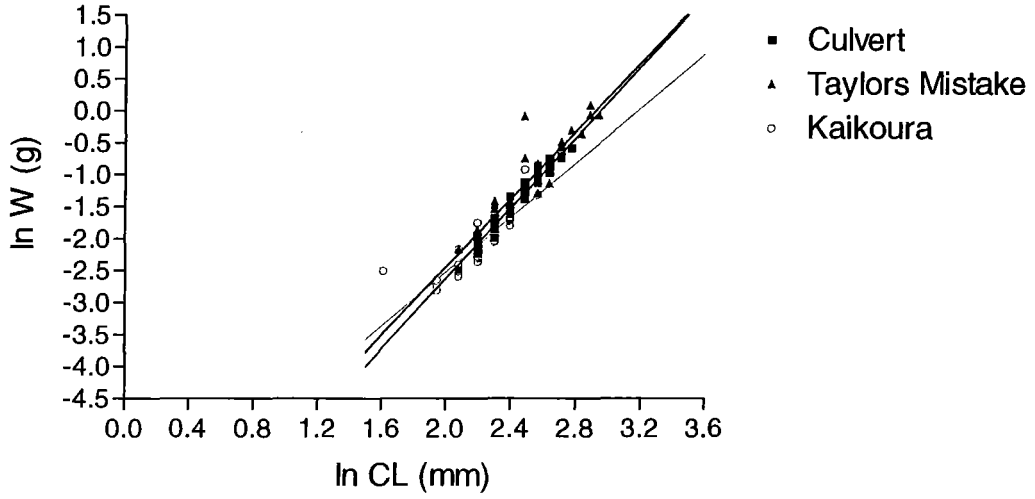


Fig. 2.12 Size of male *Palaemon affinis* collected from the Culvert, Taylors Mistake, and Kaikoura in 2000 as measured by: a, mean carapace length (CL, mm); b, mean total body length (TBL, mm); and c, mean wet weight (W, g).

Table 2.3 Parameters of linear regressions (with or without natural logarithmic transformation of both X and Y values) describing the relationships between measurements of body size (mm) and wet weight (g) of *Palaemon affinis*. Data are given for paired sites for comparison. TBL=total body length; CL=carapace length; W=wet weight; *N*=number of observations by data pairs; and r^2=coefficient of determination. Morphometric and size-weight relationships were calculated for males (M) and females (F) separately. Only relationships between sites that differed significantly are given. Slopes were statistically compared between sites with multiple ANCOVA; intercepts with ANOVA when slopes did not differ significantly. Significance is indicated with *, **, *** ($P<0.05$, $P<0.01$, $P<0.001$).

Y	*X*	*Site*	*Sex*	*Intercept*	*Slope*	*N*	r^2
Culvert and Taylors Mistake							
TBL	CL	Culvert	M	2.1537*	2.5209	47	0.9585
		Taylors	M	3.4396*	2.4264	39	0.9401
ln W	ln CL	Culvert	M	-8.1180***	2.7462	47	0.9618
		Taylors	M	-7.7400***	2.6483	39	0.8751
ln W	ln TBL	Culvert	M	-11.3464***	2.8889	47	0.9801
		Taylors	M	-11.4220***	2.9474	39	0.9487
Culvert and Kaikoura							
TBL	CL	Culvert	M	2.1537*	2.5209	47	0.9585
		Kaikoura	M	4.0680*	2.2761	49	0.8985
ln W	ln CL	Culvert	M	-8.1180	2.7462**	47	0.9618
		Kaikoura	M	-6.7719	2.1257**	49	0.7822
Taylors Mistake and Kaikoura							
TBL	CL	Taylors	M	3.4396*	2.4264	39	0.9401
		Kaikoura	M	4.0680*	2.2761	49	0.8985
ln TBL	ln CL	Taylors	F	-8.1252	2.7935	23	0.9589
		Kaikoura	F	-7.9798*	2.6813	50	0.9457
ln W	ln CL	Taylors	M	-7.7400	2.6483*	39	0.8751
		Kaikoura	M	-6.7719	2.1257*	49	0.7822
ln W	ln TBL	Taylors	M	-11.4220***	2.9474	39	0.9487
		Kaikoura	M	-10.9375***	2.7583	49	0.9348

a)



b)

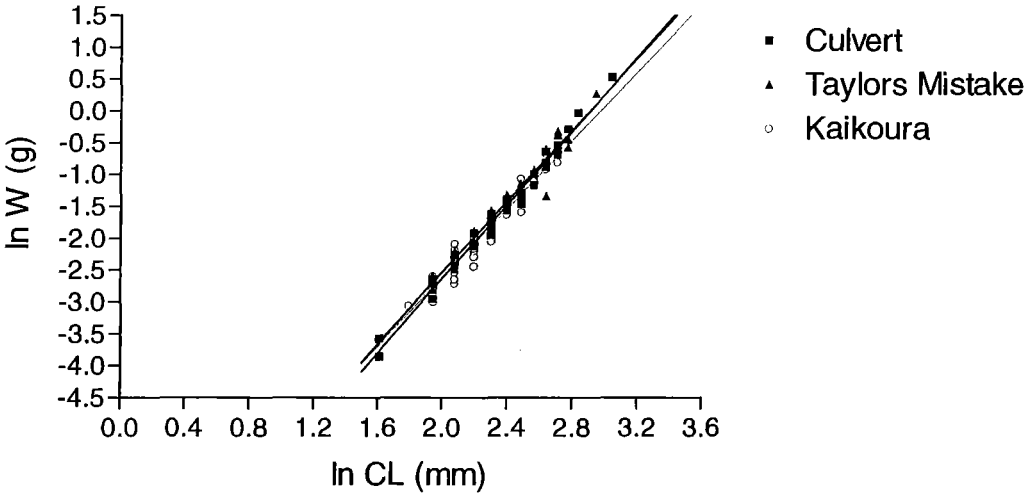


Fig. 2.13 Allometric relationship between carapace length (CL, mm, natural log transformed) and wet weight (W, g, natural log transformed) for: a, male; and b, female *Palaemon affinis* for all sites pooled.

For pooled data, sexual dimorphism was found when size was expressed as total body length, but not for carapace length or weight (Fig. 2.14). The mean TBL of all male *P. affinis* collected in this study, 26.9 ± 0.7 mm, was significantly smaller (P=0.0136) than the females, 29.5 ± 0.8 mm (Fig. 2.14b). The mean carapace length of males, 10.4 ± 0.2 mm, was similar to that of females, 10.6 ± 0.3 mm, as was the mean weight of males, 0.247 ± 0.016 g, and barren females, 0.294 ± 0.030 g (Fig. 2.14a, c).

Conversely, growth rates did not vary between male and female *P. affinis* when the data were pooled (Table 2.4). For example, when growth was examined using the linear regression equations for male and female lnW against lnTBL, similar slopes were found, male slope=2.9890 and female slope=2.9776.

Seasonal patterns occurred with size distribution of male and barren female *P. affinis* (Fig. 2.15). In general, in February to March, the population of *P. affinis* consisted mainly of medium to large size prawn. From April to September, the mean size decreased resulting in the population consisting mainly of small to medium individuals with the smallest individuals occurring in August to September. The mean size then increased in October to November, and continued to increase in December to January. Male and barren female *P. affinis* collected in December-January differed significantly in carapace length and total body length (Fig. 2.15). Males had a significantly (P=0.0051) smaller CL (12.8 ± 0.5 mm) than the females (14.8 ± 0.5 mm), as well as a significantly (P=0.0032) smaller TBL (33.7 ± 1.3 mm) than females (39.0 ± 1.1 mm). Difference in CL and TBL did not occur in other months. No seasonal differences were found in male and barren female weight.

2.4.4. Reproduction

Data on the presence of gravid females showed that *Palaemon affinis* had a definite breeding season in late spring and early summer, followed by a non-breeding season in autumn and winter (Fig. 2.4). The different populations differed slightly in the month ovigerous females were present. The first ovigerous female was collected from the Culvert during the preliminary sampling in late February 2000. This female (17 mm CL) weighed 1.025 g and carried 350 early developmental stage (non-eyed) eggs. No prawns were collected from Taylors Mistake or Kaikoura during the

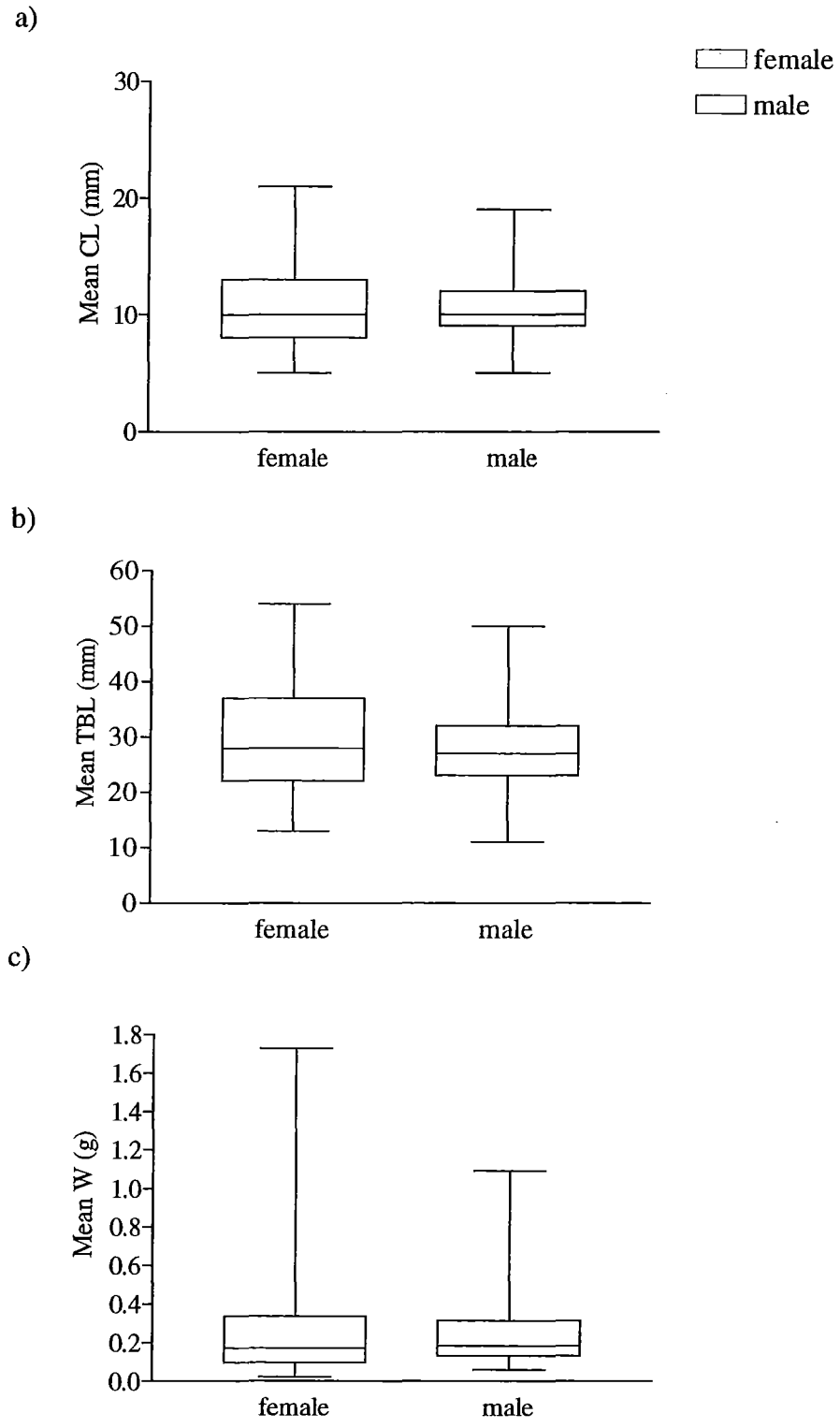
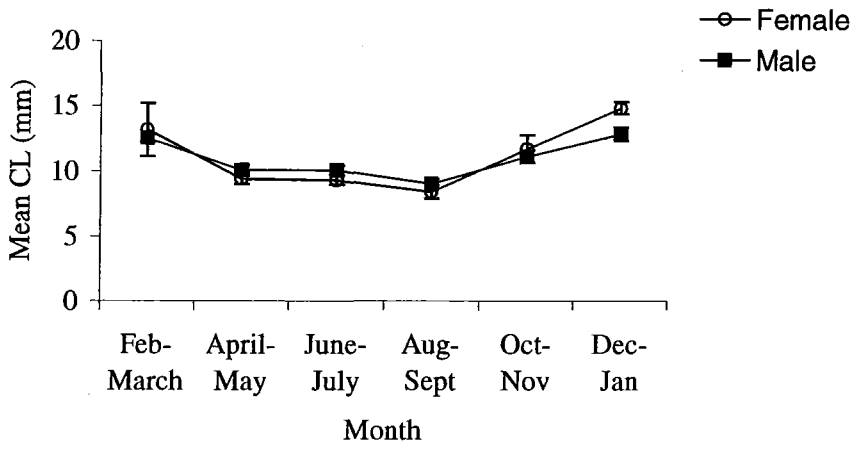


Fig. 2.14 Size range for pooled samples of male and barren female *Palaemon affinis* as measured by: a, mean carapace length (CL, mm); b, mean total body length (TBL, mm); and c, mean wet weight (W, g).

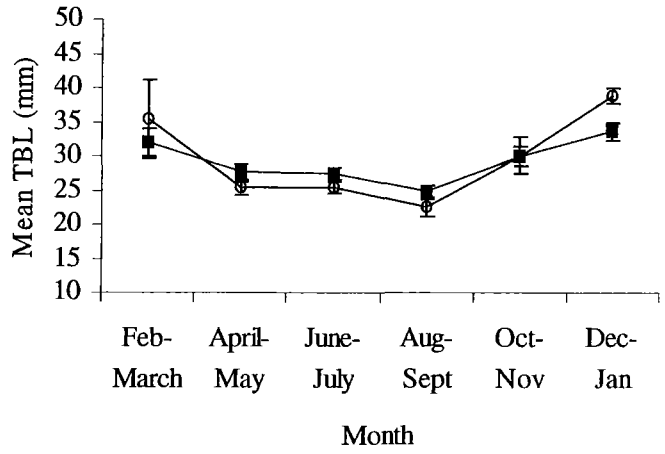
Table 2.4 Parameters of linear regressions (with or without natural logarithmic transformation of both X and Y values) describing the relationships between measurements of body size (mm) and wet weight (g) of *Palaemon affinis* from all sites pooled. TBL=total body length; CL=carapace length; W=wet weight; *N*=number of observations by data pairs; and r^2=coefficient of determination. Morphometric and size-weight relationships were calculated separately for males (M) and females (F). Slopes were statistically compared between sexes with ANOCOVA; intercepts with ANOVA when slopes were not significantly different. Significance is indicated with *, $P<0.05$. When neither slope nor intercept were significantly different, regressions for pooled data, Σ, were given.

Y	*X*	*Sex/Stage*	*Intercept*	*Slope*	*N*	r^2
Pooled data						
TBL	CL	M	2.4044*	2.4897	135	0.9519
		F	1.5817*	2.5295	112	0.9661
ln TBL	ln CL	M	1.2190*	0.9073	135	0.9421
		F	1.1382*	0.9356	112	0.9699
ln W	ln CL	Σ	-8.1532	2.7749	247	0.9396
ln W	ln TBL	M	-11.6501*	2.9890	135	0.9605
		F	-11.5641*	2.9776	112	0.9625

a)



b)



c)

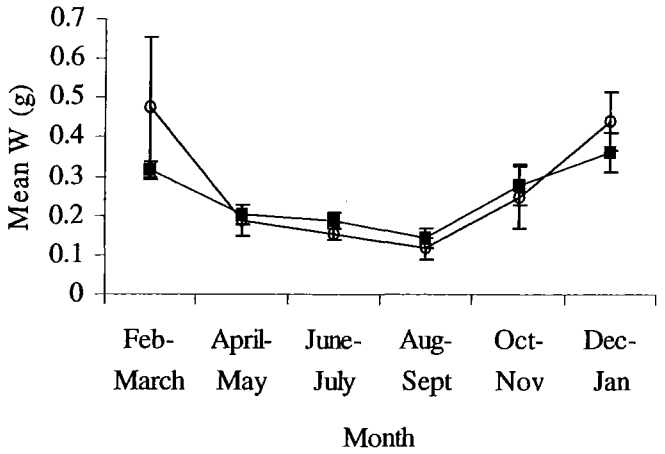


Fig. 2.15 Size range of pooled bimonthly samples of male and barren female *Palaemon affinis* as measured by: a, mean carapace length (CL, mm); b, mean total body length (TBL, mm); and c, mean wet weight (W, g).

preliminary sampling, so it is not known if ovigerous female were also present at these two sites in February.

No ovigerous females were collected from any site from March to September 2000 (Fig. 2.4). The first ovigerous female collected after this non-breeding period was a single female from Taylors Mistake in late October. This female (16 mm CL) weighed 0.966 g and carried 690 non-eyed eggs. Most ovigerous female, 15 of 17 collected during the sampling year, were collected in December. The proportion of ovigerous females in the December-January population varied between sites: 8 of 21 (38%) at the Culvert, 6 of 20 (30%) at Taylors Mistake, and 1 of 20 (20%) at Kaikoura. Therefore, ovigerous females were a significant proportion of the Culvert and Taylors Mistake populations during this period, but were less prevalent at Kaikoura.

The size at the onset of maturity (SOM) of females varied between the sites. There was some evidence that SOM may have been related to the maximum size of the females within each population. The smallest SOM (13 mm CL) recorded for a female was the individual from Kaikoura, whose population had the lowest maximum CL (15 mm) for any of the sites (Table 2.5). The largest SOM (16 mm CL) was at the Culvert, which also had the largest maximum CL (21 mm) for females for a site. The same patterns of SOM were also apparent when size was measured as total body length or weight.

Size, and weight of ovigerous females, as well as the number of eggs they were carrying differed between Kaikoura and the other two populations, but that may have been a function of the small sample size (n=1) at Kaikoura. The ovigerous female from Kaikoura was smaller (13 mm CL, 33 mm TBL, and 0.370 g) and carried fewer eggs (110) than females from the Culvert or Taylors Mistake (Table 2.5). Ovigerous females from the Culvert ranged from 16-20 mm CL, 41-53 mm TBL, 0.680-1.729 g and carried 200-650 eggs, which were themselves similar to Taylors Mistake which were 15-18 mm CL, 39-46 mm TBL, 0.624-1.024 g and carried 200-690 eggs. Conversely, the weight of the egg mass did not differ between the populations, ranging from 0.033 to 0.260 g.

The number of eggs carried by *P. affinis* was not related to the individual female's size or weight (Table 2.6). The various body size measurements, or weight, and fecundity were only weakly correlated, and the correlations were not statistically

Table 2.5 Range of carapace length (CL, mm), total body length (TBL, mm), and wet weight (W, g) of barren and ovigerous female *Palaemon affinis* collected from the Culvert, Taylors Mistake, and Kaikoura in 2000 and for pooled sites. BF = barren females; OF = ovigerous females; *N* = number of observations; SOM = size at the onset of maturity in females (expressed as the minimum CL, TBL and W); W of eggs (g); and range of fecundity (egg number).

	Culvert		Taylors Mistake		Kaikoura		Pooled Sites	
	BF	OF	BF	OF	BF	OF	BF	OF
N	39	9	23	7	50	1	112	17
CL (mm)	5-21	16-20	7-19	15-18	5-15	13	5-21	13-20
TBL (mm)	13-54	41-53	19-50	39-46	15-38	33	13-54	33-53
W (g)	0.021-1.691	0.680-1.729	0.060-1.310	0.624-1.024	0.028-0.513	0.370	0.021-1.691	0.370-1.729
SOM								
CL (mm)		16		15		13		13
TBL (mm)		41		39		33		33
W (g)		0.680		0.624		0.370		0.370
Egg W (g)		0.033-0.260		0.060-0.138		0.033		0.033-0.260
Fecundity		200-650		200-690		110		110-690

Table 2.6 Parameters of linear regressions (natural logarithmic transformation of both X and Y values) describing the relationships between measurements of body size (mm) or wet weight (g) and fecundity (number of eggs carried) of *Palaemon affinis*. Data are given for individual sites and all sites pooled. TBL=total body length; CL=carapace length; W=wet weight; FEC=fecundity; *N*=number of observations by data pairs; and r^2=coefficient of determination. Relationships were calculated for eggs with eyes or no eyes separately. Slopes were statistically compared between sites with multiple ANCOVA; intercepts with ANOVA when slopes did not differ significantly. No significant differences occurred, so regressions for pooled eyed and non-eyed egg data, Σ, were also given, which included the one ovigerous female from Kaikoura (CL=13 mm, TBL=33 mm, W=0.370 g, and FEC=110 eggs).

Y	*X*	*Sex/Stage*	*Intercept*	*Slope*	*N*	r^2
Culvert						
ln FEC	ln CL	Eyes	-9.7617	5.3678	4	0.5341
		No-eyes	11.3196	-1.9567	5	0.4072
		Σ	3.4590	0.8130	9	0.0286
ln FEC	ln TBL	Eyes	-12.2538	4.6774	4	0.5317
		No-eyes	10.9609	-1.3671	5	0.2324
		Σ	1.9609	1.0025	9	0.0530
ln FEC	ln W	Eyes	5.5249	1.4722	4	0.5569
		No-eyes	5.7133	-0.5130	5	0.3171
		Σ	5.7841	0.2528	9	0.0399
Taylors Mistake						
ln FEC	ln CL	Eyes	6.9246	-0.4137	2	1
		No-eyes	6.0090	-0.0832	5	0.0002
		Σ	6.1259	-0.1264	7	0.0005
ln FEC	ln TBL	Eyes	7.7927	-0.5391	2	1
		No-eyes	-0.4422	1.6672	5	0.0566
		Σ	0.5149	1.4065	7	0.0458
ln FEC	ln W	Eyes	5.7566	-0.1639	2	1
		No-eyes	6.0866	1.1945	5	0.3561
		Σ	5.9467	0.8664	7	0.2521
Pooled data						
ln FEC	ln CL	Eyes	-3.1889	3.1255	6	0.2992
		No-eyes	0.4776	1.8798	11	0.1633
		Σ	0.4132	1.8897	17	0.1803
ln FEC	ln TBL	Eyes	-5.9741	3.0702	6	0.3379
		No-eyes	-2.9818	2.3263	11	0.2710
		Σ	-2.4331	2.1661	17	0.2610
ln FEC	ln W	Eyes	5.6563	1.1442	6	0.4225
		No-eyes	5.9422	0.8703	11	0.3656
		Σ	5.8244	0.7129	17	0.3060

significant. Correlations were strongest for relationships of size measures when calculated using the different egg developmental stages (eyed or non-eyed), but were lower for pooled data. For example, the weight of ovigerous females from the Culvert accounted for about 56% of the variance in FEC for eyed eggs (r^2 = 0.5569, lnW against lnFEC) and nearly 32% of FEC for non-eyed eggs (r^2 = 0.3171), but the difference was not significant and, so, when correlations were recalculated using pooled data there was little relationship between female size and fecundity (r^2 = 0.0399) (Table 2.6). Correlations for pooled data from the three populations were also weak and also tended to be strongest when eyed or non-eyed eggs were treated separately, but were not as dramatically lower when data for egg type were pooled as they did for the Culvert.

2.5. Discussion

2.5.1. Distribution

The exact distribution of *Palaemon affinis* has been somewhat elusive. *P. affinis* was initially reported as having a southern circumpolar distribution until Holthuis (1952) found that records outside New Zealand were the result of erroneous identifications. The distribution of *P. affinis* has since been limited to New Zealand, but is still reported to be ubiquitous in the intertidal throughout New Zealand, and even being extremely common and abundant in the brackish reaches of the estuaries (Richardson & Yaldwyn 1958; Morton & Miller 1968). This description of the distribution appears to be based primarily on anecdotal comments in the literature not supported by data or literature citation.

In this study, *P. affinis* was found to occur in intertidal habitats on the eastern coast of the South Island, in particular, within the Avon-Heathcote Estuary, and rock pools at Taylors Mistake and Kaikoura, but the distribution was patchy and the abundance in any one site fluctuated seasonally. Within the estuary, *P. affinis* were not found at any of the other preliminary sites sampled around the Estuary. Their absence from these other sites suggests that *P. affinis* may be restricted to McCormacks Bay and associated channels. The patchiness in distribution was also observed at Taylors Mistake and Kaikoura. *P. affinis* did not occur consistently in all the rock pools at these sites. For example, at Kaikoura, prawns were uncommon in

pools higher or lower on shore than in the study pool, and were scarce in these pools during spring and autumn months. Prawns were also never collected in the low tide pools or in narrow channels open to the sea.

Kirkpatrick (1981) found that *P. affinis* within McCormacks Bay were most abundant amongst the rocks and concrete overhangs at high tide. She also found that their abundance varied over the tidal cycle: prawn numbers were lowest at low tide. Kirkpatrick (1981) suggested that the decline in abundance might be the result of *P. affinis* moving at low tide to the deeper channel directly in front of her study site, or being swept through the culvert with the out-flowing tide, returning again with the in-coming tide. Jones (1983) went further, suggesting that *P. affinis* leave the estuary and return with the next in-coming tide.

In this study, *P. affinis* were collected in the Culvert channel draining the eastern part of McCormacks Bay into the main body of the estuary at low tide, which supports Kirkpatrick's (1981) suggestion that *P. affinis* moved to the deeper channels at low tide. However, a steep gradient in abundance was found within the Culvert channel, such that prawn numbers were highest near the culvert (where the current was strongest) and dwindled to none at the point where the Culvert channel reached the main low channel of the Heathcote and Avon Rivers.

Additionally, the abundance of *P. affinis* fluctuated over the year; for example, at the Culvert, peak numbers were collected in June-July, but none were found in October-January. The fluctuations in abundance may result from the migration of the prawns, as suggested by Jones (1983), but is more likely to be an artefact of the sampling method. In June-July, when this study found prawns to be most abundant in the Culvert channel, Kirkpatrick (1981) collected no *P. affinis* amongst the rocks at high tide during the day and only low numbers at night. These observations suggest that *P. affinis* may inhabit different shore levels during the course of the year. However, the apparent variation in seasonal abundance may also be an artefact of the sampling methods in the different studies. Peak numbers were collected with the suction sampler in winter, but none in summer. *P. affinis* was collected in the Culvert channel in December by a hand-trawled net, but whether the net would have caught prawns there in October cannot be determined as no net was available at that time. In winter, *P. affinis* appeared to move more slowly, possibly as a result of the cooler

water temperatures, which may have allowed more prawns to be captured. With the higher temperatures in summer, the prawns were more active and may have been able to avoid capture. However, some poikilotherms, especially intertidal invertebrates, are able to compensate for the effect of changing temperature on their metabolism (Florkin 1960; Bartholomew 1977). If this were the case then activity in *P. affinis* would be equal regardless of the season. The distribution of *P. affinis* in time and space is not well understood, and the general statements in the current literature certainly do not agree with the results of this study.

As with *P. affinis*, many other species of *Palaemon* are found in estuaries and intertidal rock pools. Populations of *Palaemon serratus* (Forster 1951; Bamber & Henderson 1994), *P. elegans* (Rodriguez & Naylor 1972), *P. serenus* (Walsh & Mitchell 1998), *P. longirostris* (Marchand 1981; Fincham & Furlong 1984; Attrill & Thomas 1996), *P. montagui* (Attrill & Thomas 1996), and *P. styliferus* (Subrahmanyam 1975) have been reported from estuaries around the world. In addition, populations of *P. serratus* and *P. elegans* have also been reported from intertidal rock pools (Rodriguez & Naylor 1972), as have *P. northropi* (Anger & Moreira 1998) and *P. pacificus* (Emmerson 1985). *Palaemon* species however are not limited to these habitats, and have been reported in shallow seagrass meadows (*P. serratus, P. xiphias, P. adspersus*) (Guerao & Ribera 2000), on sandy mud flats near mangrove areas (*P. northropi*), as well as in freshwater habitats (*P. pandaliformis*) (Anger & Moreira 1998).

Seasonal fluctuations in abundance are common in species of *Palaemon*. Fluctuations in abundance of resident populations of *P. elegans* (Rodriguez & Naylor 1972) and *P. xiphias* (Guerao & Ribera 1996) were suggested to have resulted from recruitment, which may also be the case for the *P. affinis* population at Kaikoura in this study.

Conversely, changes in seasonal abundance of many other *Palaemon* species are suggested to result from migration, as resident populations were not found in the selected habitats. Migrations have been suggested for *P. serratus* (Forster 1951; Rodriguez & Naylor 1972; Bamber & Henderson 1994; Guerao & Ribera 1996), *P. longirostris* (Marchand 1981; Attrill & Thomas 1996), *P. styliferus* (Subrahmanyam 1975), *P. macrodactylus* (Sitts & Knight 1979), and possibly *P. affinis* from Taylors

Mistake (present study). However, little is known about these apparent changes in the prawn's abundance. Bamber & Henderson (1994) suggested that *P. serratus* from the Severn Estuary, UK may have migrated in response to changes in salinity. Rodriguez & Naylor (1972) suggested *P. serratus* from Oxwich, Gower, UK may have migrated to avoid cooler water temperatures in winter; while Sitts & Knight (1979) suggested *P. macrodactylus* migration may be in response to changes in the frequency of predation. As many physical variables, such as light, salinity, water temperature, and substratum, as well as biotic variables, such as growth, feeding, sexual maturation, and possibly density may be related to migratory behaviour (Guerao & Ribera 2000), further research is needed before the existence of migrations can be confirmed and the reasons for any migrations can be understood.

2.5.2. Sex ratios

The sex ratios found were comparable to those reported by Kirkpatrick (1981), who found skewed sex ratios in the medium and large size classes of *P. affinis* from McCormacks Bay. The medium size class was dominated by males, and the large the by females. However, Kirkpatrick (1981) used different size class parameters than used here for the Culvert channel, which drains McCormacks Bay. Kirkpatrick (1981) defined "small" as 7-12 mm carapace length (CL), "medium", 13-17 mm CL, and "large", 18-26 mm CL, which were all larger than here (small, 5-8 mm CL; medium, 9-14 mm CL; and large, 15-21 mm CL). The differences may result from the effects of different periods, frequency, and methods of collection. Kirkpatrick (1981) collected *P. affinis* with a triangular dipping net from February to July 1981, whereas I collected *P. affinis* using a suction sampler from February to December 2000. If an influx of smaller individuals as happened in August 2000 had occurred in 1981, Kirkpatrick (1981) would not have collected the smaller individuals. Additionally, if Kirkpatrick (1981) collected more frequently than was done in 2000, she may have collected more of the larger individuals that are present in summer, which would have increased the sample size at the top of the size range, exacerbating the differences in size classes between the studies. Furthermore, the methods of sampling used in each study may have differed in their ability to catch particular size classes.

Kirkpatrick (1981) also found a "normal" sex ratio in the small size class of *P. affinis*: the sex ratio of individuals 8-12 mm CL was 1: 1. Similarly, Campbell & Jones (1989) found a 1: 1 sex ratio in *Palaemon longirostris* for the small individuals, whereas males dominated the medium size class and females the large. Both these observations contrast with the results of the present study, in that the sex ratios of small individuals in all sites were skewed, possibly the resulting from individuals below the minimum externally sexable size of males in this size class.

Kirkpatrick (1981) suggested the skewed sex ratio in size classes of *P. affinis* might result from *P. affinis* undergoing a double sex reversal. She suggested that most females become male when they reach 12-13 mm CL, and then change back to female at 16 mm CL. Because the dimensions of size classes in the two studies and in the different populations were different, it does not seem likely that *P. affinis* undergoes a sex reversal at any particular size, but that the observations of differing sex ratios for different size classes might be related to the maximum body size in the population, and not the changes within the population.

Wenner (1972) suggested that skewed sex ratios might also result from sexual differences in longevity, migration, mortality, or growth. Based on the patterns of growth observed in my study, another plausible reason for the skewed sex ratios in the medium and large size classes is the difference in the final size of male and female *P. affinis*. Male and female prawns from the Culvert differed in size and weight, but males and females were generally the same size during the non-breeding season and females larger than the males were typically caught only during the breeding season. Male prawns may moult before females to facilitate reproduction, as copulation occurs between a non-moulted male and a recently moulted female in most prawns (Conan 1985). An earlier moulting would result in less time to accumulate energy resources to allocate to growth, resulting in a smaller maximum size in male prawns. Regardless of the underlying causes, whether *P. affinis* undergoes sex reversal cannot be determined using the data from either this study or in Kirkpatrick (1981), and a detailed study focusing on the ontogeny of individual prawns would be required to determine if sex change or changes occur in *P. affinis*.

2.5.3. Growth

The size range of *P. affinis* observed in the three sites in 2000 agreed with other studies (Yaldwyn 1954; Kirkpatrick 1981), but were at the lower end of the reported length ranges. For example, Kirkpatrick (1981) reported the size range of *P. affinis* from McCormacks Bay as 6-26 mm carapace length, CL, whereas, the largest prawn recorded in this study from the Culvert was only 21 mm CL. Richardson & Yaldwyn (1958) reported *P. affinis* with lengths up to ~ 75 mm, but the largest prawn found at any of the three sites in 2000 was only 54 mm total body length, TBL. Richardson & Yaldwyn (1958) make a reference to the prawns being abundant in the brackish waters and mangrove swamps of the north. It may be that Richardson & Yaldwyn (1958) were studying prawns from a northern population, where water temperatures are likely to be higher than those here, and greater growth rates might allow the species to reach a greater size. Conversely, it might be expected that the southern populations, in colder more productive water, might be larger. The smaller prawns recorded in this study might be an artefact of the sampling sites or the sampling techniques, and until more is known about geographical variation over a larger scale, the basis for the differences cannot be determined.

As has been reported for other species of *Palaemon*, *P. affinis* showed sexual dimorphism in size (when expressed at total body length), but not in their rate of growth. Male and female *Palaemon northropi* Rankin and *P. pandaliformis* Stimpson increased in size (both length and weight) at similar rates, but attained different body sizes and weight (Anger & Moreira 1998), as did *P. elegans* Rathke (Hartnoll & Salama 1992). Growth patterns of the sexes also differed in other species of *Palaemon*, such as *P. serratus* Pennant (Guerao & Ribera 2000) and *P. xiphias* Risso (Guerao *et al.* 1994).

Additionally, the growth rates of male and female *P. affinis* were similar to those of other species of *Palaemon* (Table 2.7). The relationship between total body length and wet weight in male *P. affinis* had a slope of 2.99, which was well within the range of 2.56-3.29 for other male *Palaemon* as reported by Guerao *et al.* (1994), Anger & Moreira (1998), and Guerao & Ribera (2000). For females, the slope relating total body length to wet weight for *P. affinis* was, at 2.98, similar to 2.86 for *Palaemon elegans* (Hartnoll & Salama 1992). However, the values were slightly less

Table 2.7 Slope parameters of the allometric size-weight relationship (linear after ln-ln transformation of size and weight data) in several *Palaemon* spp.; given separately for males and females where data are available, otherwise for pooled data, Σ; size measured as total body length (TBL: except for Hartnoll & Salama 1996; carapace length, CL); and wet (W) or dry (DW) weight.

	Slope					
Species	Males	Σ	Females	Size	Weight	Reference
Palaemon affinis Milne-Edwards	2.99		2.98	TBL	W	Present study
P. serratus Pennant	2.56		3.11	TBL	W	Guerao & Ribera (2000)
P. northropi Rankin	3.29		3.61	TBL	DW	Anger & Moreira (1998)
P. pandaliformis Stimpson	3.02		3.06	TBL	DW	Anger & Moreira (1988)
P. xiphias Risso	2.97		3.14	TBL	W	Guerao *et al.* (1994)
P. elegans Rathke		2.86		CL	W	Hartnoll & Salama (1992)

than that for females of other *Palaemon* species, which varied from 3.06 to 3.61 (Guerao *et al.* 1994; Anger & Moreira 1998; Guerao & Ribera 2000).

2.5.4. Reproduction

The breeding season of *P. affinis* observed at the study sites in 2000 agrees with that reported by Yaldwyn (1954) and Richardson & Yaldwyn (1958), but the breeding season in Canterbury and Marlborough was slightly shorter. Yaldwyn (1954) and Richardson & Yaldwyn (1958) reported ovigerous females of *P. affinis* from September to March, whereas, ovigerous females were collected in this study only from October to February. The months that ovigerous females were collected also varied among the three populations, with one ovigerous female being collected in October from Taylors Mistake, but none from either the Culvert or Kaikoura.

Guerao *et al.* (1994) noted that the reproductive cycle of many crustaceans depends on particular environmental conditions, especially temperature, day length, and food supply. The reproductive cycle of *P. affinis* in the north-eastern South Island may be related to water temperature. In October, Taylors Mistake had the highest temperature, 25°C, of the three sites, whereas the water temperature at the Culvert and Kaikoura was only 20°C. Also, larger numbers of ovigerous females were collected in December at Taylors Mistake and the Culvert when water temperature was relatively high (24.5°C and 22°C, respectively) and only a single ovigerous female was collected at Kaikoura in December, when the water temperature had fallen to 15°C. The sum of daily temperatures rather than instantaneous changes in temperature may influence moulting (Conan 1985), which is essential for copulation in many prawns as copulation occurs soon after the female has moulted (Hartnoll 1985). This relationship between temperatures and moulting suggests that the onset of breeding in *P. affinis* may require temperatures greater than 20°C for some (unknown) minimum period. The possible dependence of the reproductive cycle on temperature would be an interesting topic for future research.

The size at onset of maturity (SOM) of female *P. affinis* was similar to that recorded for other *Palaemon* species. For example, Guerao *et al.* (1994) reported female *P. xiphias* reached maturity at 37.9 mm total body length, TBL, in late spring to early summer. Likewise, *P. pacificus* became sexually mature at 41 mm TBL in

late summer-early autumn (Emmerson 1985). The range of SOM, 33-41 mm TBL, of female *P. affinis* from the three study populations agree with other species of *Palaemon*. Egg numbers were also similar to those in other *Palaemon*. For example, the range for *P. affinis* (110-690 eggs) encompassed those recorded for *P. northropi* Rankin (172-418 eggs), and *P. pandaliformis* Stimpson (102-375 eggs) (Anger & Moreira 1998). These numbers appear however to be at the lower end of the range of egg numbers which species of *Palaemon* can carry. *P. pacificus* has been reported carrying up to 1,786 eggs (Emmerson 1985), while *P. xiphias* carries as many as 2,750 eggs (Guerao *et al.* 1994).

Apart from these similarities, the reproductive strategy of *P. affinis* differed from that in other species of *Palaemon*. In several species of *Palaemon*, the number of eggs carried was related to the size of the ovigerous female (Emmerson 1985; Guerao *et al.* 1994; Anger & Moreira 1998). In contrast, the number of eggs carried by *P. affinis* was not related to the size of the ovigerous female. Body size and fecundity were weakly correlated for all the measures of size employed. For the linear relationship of TBL against FEC, the slope, 2.17, for *P. affinis* was much lower than that for other species of *Palaemon* (Table 2.8); the least slope, 2.53, was recorded for *P. pandaliformis* (Anger & Moreira 1998), but slopes as great as 3.59 were recorded for *P. xiphias*. This means that the number of eggs carried by a female increased at a lower rate in relation to body size with increasing body size in *P. affinis* than in other species of *Palaemon*.

When stages of egg development were factored in, the relationships between size and fecundity were more evident (slope of size against fecundity for females with eyed eggs, 3.07, slope of those within non-eyed eggs, 2.33) and closer to the range of other *Palaemon* but still below the minimum range for those taxa. The weak correlation between body size and fecundity in *P. affinis* may be related to the small number of ovigerous female collected or to the small size range of the ovigerous females. Few ovigerous females were collected (17 total) which is substantially less than samples in other literature. For example, relationships between fecundity and body size for *P. pandaliformis* were calculated using 75 individuals (Anger & Moreira 1998).

Table 2.8 Slope parameters of the allometric size-fecundity relationship (linear after ln-ln transformation of size and fecundity, expressed as the number of eggs) in several *Palaemon* spp.; size was measured as total body length (mm).

Species	Slope	Habitat	Reference
Palaemon northropi Rankin	2.70	Marine	Anger & Moreira (1998)
P. pacificus Stimpson	2.60	Marine	Emmerson (1985)
P. xiphias Risso	3.59	Marine	Guerao *et al.* (1994)
P. affinis Milne-Edwards	2.17	Marine-estuarine	Present study
P. pandaliformis Stimpson	2.53	Freshwater-estuarine	Anger & Moreira (1998)

Obviously, the 17 ovigerous females collected may not have been representative of the entire population and there was a small size range of ovigerous *P. affinis* (13-20 mm CL). Anger & Moreira (1998) reported weak correlations between body size and fecundity in *Palaemon northropi*, and suggested this was the result of the small size range of the ovigerous female in that species, which, as noted, may well also apply to *P. affinis*. Further research focusing on the reproductive biology of *P. affinis* using a much larger sample size is required to determine the reproductive strategy of *P. affinis*.

Chapter Three

Community and Natural Food Preferences of *Palaemon affinis*

Chapter Three: Community and Natural Food Preferences of *Palaemon affinis*

3.1. Introduction

The *Palaemon affinis* community has not been described in detail for any habitat in New Zealand and the species' interactions within the communities are unknown. Knowledge of the natural diet of *P. affinis* is important to developing an understanding of the interactions of the prawn with other organisms within the community. Also, the composition of the fauna in each habitat will determine the food items available to the prawn and may account for local differences in distribution patterns. Despite the prawns obvious ability to tolerate a range of salinities that would allow it to live almost anywhere in the estuary or the adjacent ocean (Kirkpatrick 1981; Kirkpatrick & Jones 1985), *P. affinis* may be confined to habitats and communities with certain food (or prey). This chapter introduces the communities of which *P. affinis* is a part on the Canterbury and Marlborough coastline, and its food preferences.

The community structure was analysed by comparing the resemblances and differences in species abundance from three locations sampled on 5 (rock pool sites) and 6 (estuary) occasions. Community data are presented separately for hyperbenthic and benthic communities, even though the two communities probably have species in common. This results from the movement of hyperbenthic animals between the hyperbenthos and benthos, and by the inclusion of some benthic animals which were inadvertently sampled by the suction sampler. Several key environmental variables were also assessed to try to relate with patterns of seasonal distributions between populations.

Little has been published on the natural food preferences of *P. affinis*. Morton & Miller (1968) and Jones (1983) state that *P. affinis* is a scavenger, feeding on both dead plant and animal material. However, these suggestions were not supported by reliable data. Here, I present data on the natural food composition of different size classes of male and female *P. affinis* over a year. The results are presented as a percentage of stomachs containing a particular food item because, as with many crustaceans, the degree of precision is probably low because material is comminuted by the gastric mill (Williams 1981; Guerao 1995; Guerao & Ribera 1996). In addition, the soft parts of most food items become unrecognisable soon after

ingestion, whereas it takes longer to digest hard parts, such as setae or spicules. Thus the presence of recognisable hard parts may inflate the relative importance of such hard food items. However, the important food items, being eaten in greater quantities, are probably always more readily distinguishable from the less important food items (Williams 1981).

3.2. Methods

3.2.1. Collection of hyperbenthic and benthic communities

The collection methods used to sample the hyperbenthic communities are described in Chapter Two, Section 2.3.2. Five randomly located suction samples were taken bimonthly in February (at the estuary only), May, early June, early August, late October and early December in 2000. The hyperbenthic samples were preserved in seawater and 10% formalin in the field, separately from individuals of *Palaemon affinis*.

Benthic communities were also sampled because species in those communities possibly figure prominently in the diet of *P. affinis*. The benthos was sampled with a corer (for the soft substratum in the estuary Culvert channel) or a quadrat (hard substratum) at low tide, every two months when prawns were collected. The corer was a metal cylinder, 130 mm internal diameter, sampling a surface area of 0.0134 m^2 to a maximum depth of 173 mm. The corer was pushed into the soft sediment and removed with its contents by excavating down one side with a trowel and then sealing the bottom with the trowel as the cylinder was removed. The contents were then washed through a 0.5 mm mesh sieve and the organisms retained on the sieve were preserved in 10% formalin in the field. Two randomly located core samples were taken at each bimonthly sampling of the eastern culvert channel draining McCormacks Bay. Hard bottom benthic communities were sampled using a 115 mm square quadrat placed randomly at two places in the rock pool at each sampling. Organisms, including algae, within the quadrat were scraped off the substrate surface using a knife and preserved in 10% formalin in the field.

All community samples were sorted in the laboratory. Organisms were identified to major taxon and counted. The sorting was not done under a microscope. However, Coleman (1980) found that re-sorting a sample increased the number of

species recorded by about 13% and the number of individuals by about 37%, so each sample was re-sorted at least twice, and sometimes up to five times depending on the amount of detritus present. After sorting, animals were identified to species level or to the most detailed taxonomic level using a dissecting microscope (6.3x to 40x) and a compound microscope (40x to 400x) when necessary to discern characteristics. They were then transferred to 70% alcohol for preservation and storage. Identification was done using Knox (1951), Morton & Miller (1968), Fauchald (1977), Powell (1979), Ayling & Cox (1982), Jones (1983), McLay (1988), and McLay (1995). Dr. Graham Fenwick (National Institute of Water and Atmospheric Research, Christchurch) identified the amphipods.

3.2.2. Natural food preferences of *Palaemon affinis*

After prawns collected during bimonthly sampling (Chapter Two, Section 2.3.2) had been sexed and measured, the stomach was removed and the entire contents were washed onto a microscope slide and examined under dissecting (6.3x to 40x) and compound (40x to 400x) microscopes. Percentage fullness of each stomach was estimated visually. Items in the stomach were identified to the lowest taxonomic categories possible: unidentifiable matter, plant material, polychaetes, gastropods, bivalves, isopods, amphipods, ostracods, sponge spicules, sand grains, and crab. Food items had been fragmented, so items could not be identified to species level. Percentage occurrence of food items was determined as in Hyslop (1980) and Williams (1981) using the equation:

$$\text{Percentage occurrence for the } i\text{th prey} = \frac{b_i}{n} \times 100$$

where b_i is the number of prawns whose stomachs containing the food item i, and n is the number of prawns in the sample with a $\geq$ 50% full stomach.

3.2.3. Statistical analysis

Community samples were analysed using the proprietary software PRIMER®. Species data matrices were determined using the number of individuals of each species within each bimonthly sampling for either hyperbenthic or benthic

communities. To determine (dis) similarities in community composition between samples and sites, Bray-Curtis similarity indices were calculated between all pairs of bimonthly samples in the production data matrix after standardisation and square root transformation. These data were then ordinated using either cluster analysis or non-metric multi-dimensional scaling (MDS) to produce plots representing the similarity between samples and sites. *A priori* tests of the differences between similarity between sites and samples were done using ANOSIM (analysis of similarity) and between taxonomic groups using SIMPER (similarity percentages). To determine which environmental variables were most closely related to similarities in community composition, Spearman's Rank Correlation values between biotic and abiotic similarity matrixes were determined using the BIO-ENV option.

Natural food preferences were analysed using the statistical software package PRISM®. All data were tested for deviations from Gaussian normality with the Kolmogorov-Smirnov (KS) test before any statistical analysis. Data were arc-sine transformed and frequency of occurrence percentages calculated for males and females, size classes, and seasons. Statistical analysis between all variables, including sex, size class, season and site, were done using either One-way ANOVA (analysis of variance) or two-tailed Student's *t* tests.

3.3. Results

3.3.1. The "*Palaemon affinis* community"

3.3.1.1. The hyperbenthic community

Although the *Palaemon affinis* populations examined in this study occurred in two different habitats (rock pools and estuarine mud flats), all hyperbenthic communities were similar to some extent (similarity indices of ≥17.3%) (Fig. 3.1). Measured by similarity and dissimilarity indices, the level of similarity varied with different combinations of samples and sites. However, as expected the intra-site comparisons were generally most similar, followed by comparisons of different samples from the rock pools, and least similar were the samples from rock pools and the estuary (Fig. 3.1, 3.2).

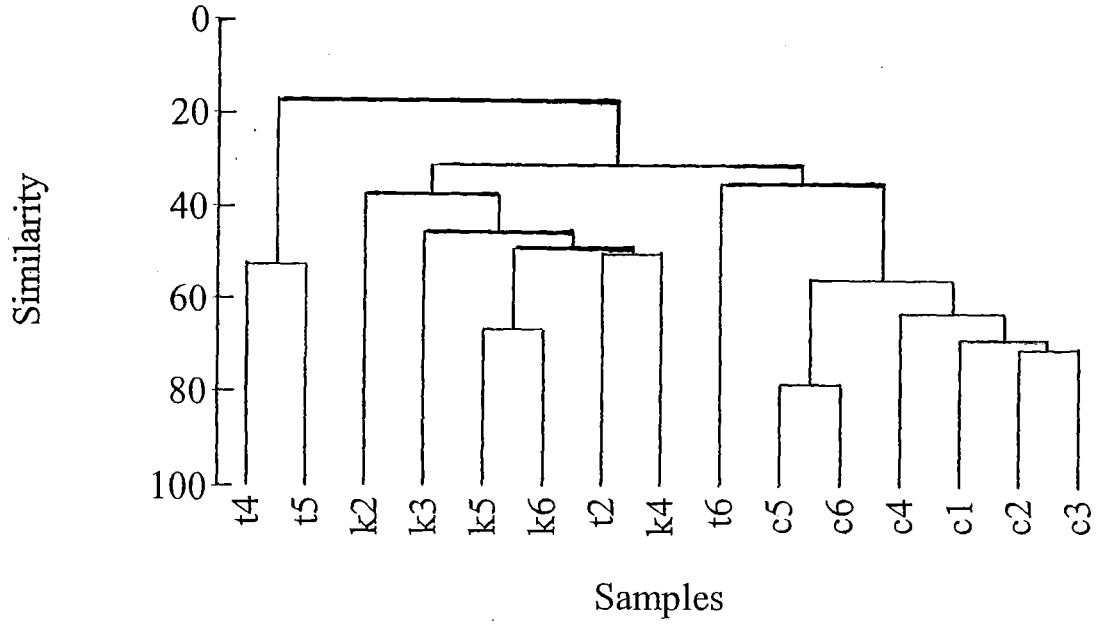


Fig. 3.1 Group-average clustering from Bray-Curtis similarities of hyperbenthic samples collected by suction sampler from the Culvert, Taylors Mistake, and Kaikoura in 2000. Culvert – c1, February-March; c2, April-May; c3, June-July; c4, August-September; c5, October-November; c6, December-January. Taylors Mistake – t2, April-May; t4, August-September; t5, October-November; t6, December-January. Kaikoura – k2, April-May; k3, June-July; k4, August-September; k5, October-November; k6, December-January.

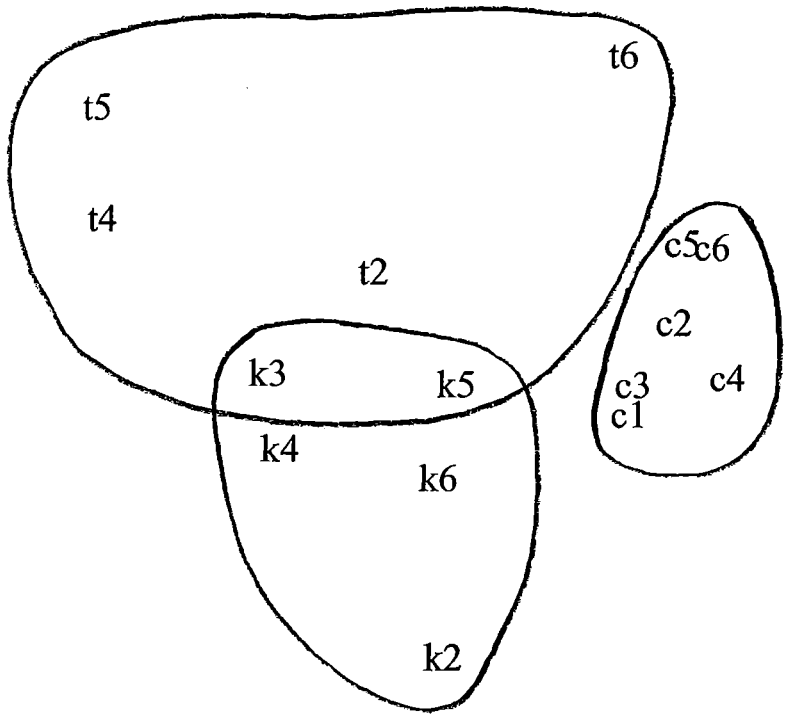


Fig. 3.2 MDS plot for samples of hyperbenthic communities at the Culvert, Taylors Mistake, and Kaikoura collected by suction sampler in 2000. Culvert – c1, February-March; c2, April-May; c3, June-July; c4, August-September; c5, October-November; c6, December-January. Taylors Mistake – t2, April-May; t4, August-September; t5, October-November; t6, December-January. Kaikoura – k2, April-May; k3, June-July; k4, August-September; k5, October-November; k6, December-January.

Similarity between intra-site samples was greatest for those from the Culvert (55.9-78.4% similar) (Fig. 3.1) because of both low variation between species abundance and faunal composition between seasons and the open nature of the site which allowed the suction sampler to take comparable samples. The results suggest that the estuarine community was more stable in composition of the two, in comparison with rock pools in general. No seasonal patterns were apparent between the samples from the Culvert, but the samples from the spring and early summer (c5 and c6, October to January) were most similar (Fig. 3.1, 3.2), which suggests that some species were less abundant in autumn and winter.

Species commonly collected with the suction sampler at the Culvert were the gammarid amphipod *Paracalliope novizelandiae*, the crabs *Halicarcinus varius*, *Hemigrapsus crenulatus*, and *Macrophthalmus hirtipes*, in addition to some benthic species such as the topshell *Micrelenchus tenebrosus*, and the sea anemone *Diadumene neozelandica* which could be removed from the substratum by the inrush of the water stream entering the cylinder. The Culvert hyperbenthic community samples were dominated, in terms of abundance, by the amphipod *Paracalliope novizelandiae*. High numbers of the gammarid amphipod were collected at all times of the year, in numbers corresponding to population densities of 710-18,284 individuals per m^2. Conversely, the numbers of *P. affinis* collected with the suction sampler varied widely; none was collected at some samplings throughout the year.

At Taylors Mistake, the hyperbenthic community appeared to be less stable than the Culvert, as the abundance of most species varied more throughout the year: intra-site samples were only 17.3-52.8% similar (Fig. 31.). Even though samples tended to vary with the season, no overall seasonal pattern was apparent (Fig. 3.2). Samples from the late winter (t4, August-September) and spring (t5, October-November) were most similar. The early summer sample (t6, December-January) had the least similarity (17.3%) to these samples (t4, t5) (Fig. 3.1).

As at the Culvert, gammarid amphipods dominated the Taylors Mistake hyperbenthic samples, but the population density was apparently much lower: the number of amphipods collected from the rock pool represented densities of 73-661 individuals per m^2. However, no species was consistently collected from the Taylors Mistake rock pools throughout the year. Samples were usually dominated by the

catseye *Turbo smaragdus*, a saccocirrid polychaete, *Palaemon affinis*, the half-crab *Petrolisthes elongatus*, and the hermit crab *Pagurus novizealandiae*.

The hyperbenthic community at Kaikoura was also less stable than that at the Culvert, but it was more stable in composition through the year than the pools at Taylors Mistake: intra-site samples from the Kaikoura pool were 37.4-66.6% similar (Fig. 3.1). No seasonal pattern was apparent between the samples, but as with the Culvert, the spring and early summer samples (k5 and k6, October-January) were the most similar (Fig. 3.1, 3.2).

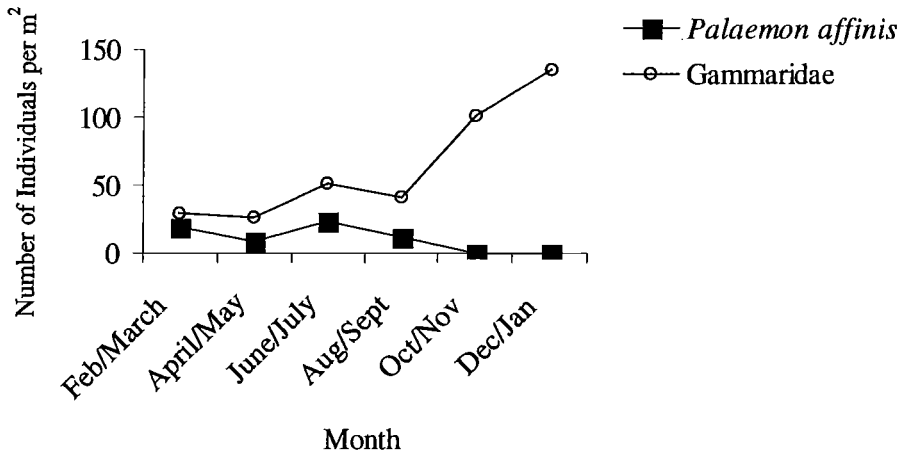
Species abundance at Kaikoura was comparable to that at Taylors Mistake except the species composition of the samples was more consistent throughout the year. As with the other two sites, gammarid amphipods dominated the hyperbenthic samples, but other common species in the samples were *Palaemon affinis*, the crab *Halicarcinus varius*, the whelk *Cominella glandiformis*, the spire snail *Zeacumantus subcarinatus*, and the topshell *Melagraphia aethiops*.

The abundance of gammarid amphipods and *P. affinis* commonly fluctuated in parallel through the year at all three sites. For example, at Kaikoura, gammarid amphipods and *P. affinis* abundance were average in April-May 2000 (Fig. 3.3). In June-July, abundance of both species increased, then decreased dramatically in August-September. Numbers of both species rapidly increased in October-November, only to decline again in December-January.

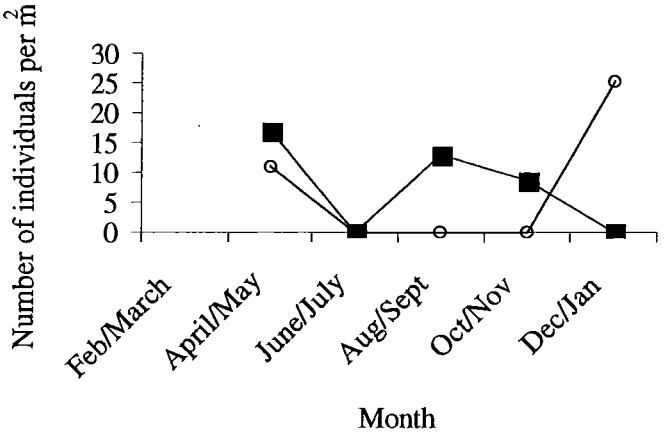
When *P. affinis* was found in the communities, the three sites shared only 8 species in common, from the range of species (≥47) collected with the suction sampler (Table 3.1). The 8 species consisted of 2 molluscs (*Melagraphia aethiops* and *Notoacmea* sp.), 2 polychaetes (*Haploscoloplos cylindrifer* and Nereidae), a crab (*Halicarcinus varius*), an amphipod (Gammaridae), an isopod (Sphaeromatidae), and a brittle star (*Amphiura hinemoa*).

Similarities between the species composition and their levels of abundance within a population and dissimilarities between the communities were calculated using the SIMPER option in PRIMER® to determine which species contributed most to the resemblances in composition of the *Palaemon affinis* community.

a)



b)



c)

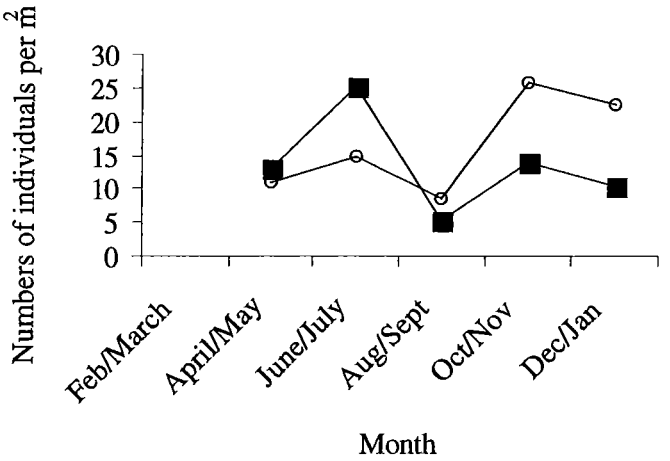


Fig. 3.3 Seasonal abundance in 2000 (individuals per m², square root transformed) of *Palaemon affinis* and gammarid amphipods collected from: a, the Culvert; b, Taylors Mistake; and c, Kaikoura.

Table 3.1 Species identified in bimonthly hyperbenthic and benthic samples collected at the Culvert, Taylors Mistake (Tay. M.), and Kaikoura in 2000. Presence of species is indicated by "X".

Species	Site		
	Culvert	Tay. M.	Kaikoura
Diadumene neozelandica (anemone)	X		
Actinia tenebrosa (beadlet anemone)			X
Tethya aurantium (golf-ball sponge)			X
Notoplana australis (flatworm)	X		
Chiton pelliserpentis (snakeskin chiton)	X	X	
Cellana strigilis redimiculum (limpet)		X	
Notoacmea sp. (limpet)	X	X	X
Melagraphia aethiops (topshell)	X	X	X
Micrelenchus sp. (topshell)	X	X	
Turbo smaragdus (catseye)		X	X
Nodilittorina antipodum (periwinkle)		X	X
Risselopsis varia (discoid snail)			X
Zeacumantus subcarinatus (spire snail)	X		X
Cominella glandiformis (whelk)	X		X
Cominella maculosa (whelk)	X		X
Mytilus edulis aoteana (blue mussel)		X	
Tellina liliana (bivalve)	X		
Protothaca crassicosta (bivalve)		X	X
Austrovenus stutchburyi (cockle)	X		
Haploscoloplos cylindrifer (polychaete)	X	X	X
Scolecolepides benhami (polychaete)	X		X
Aonides trifidus (polychaete)	X		
Polydora sp. (polychaete)	X		X
Prionospio pinnata (polychaete)	X		X

Species	Site		
	Culvert	Tay. M.	Kaikoura
Heteromastus filiformis (polychaete)	X		
Armandia maculata (polychaete)	X	X	
Lepidonotus jacksoni (scale polychaete)	X		X
Nereidae (polychaete)	X	X	X
Glycera americana (polychaete)	X		
Pectinaria australis (polychaete)	X		
Cirratulidae (polychaete)	X		X
Owenia sp. (polychaete)	X		
Saccocirridae (polychaete)	X	X	
Unidentified polychaetes		X	X
Elminius modestus (barnacle)	X		
Palaemon affinis (prawn)	X	X	X
Petrolisthes elongatus (half-crab)		X	
Pagurus novizealandiae (hermit crab)		X	
Halicarcinus whitei (pill-box crab)	X		
Halicarcinus varius (pill-box crab)	X	X	X
Hemigrapsus crenulatus (grapsid crab)	X		
Macrophthalmus hirtipes (grapsid crab)	X		
Gammaridae (amphipod)	X	X	X
Sphaeromatidae (isopod)	X	X	X
Amphiura hinemoa (brittle star)	X	X	X
Patiriella regularis (cushion star)		X	
Pseudolabrus celidotus (spotty)	X		
Tripterygion sp. (triple fin)			X

In general, gammarid amphipods contributed the most to the similarity of each population. The gammarid *Paracalliope novizelandiae* was responsible for 55.4% of the similarity index between the hyperbenthic samples collected from the Culvert (Table 3.2). Similarly, another gammarid amphipod at Kaikoura was responsible for 42.2% of the similarity between samples there (Table 3.3); and contributed most to the statistic at both sites. However, amphipods were less important in the rock pools at Taylors Mistake (9.9%), but were still the third highest contributor to the similarity between samples from the pool community (Table 3.4).

Palaemon affinis was responsible for a high percentage of similarity calculated between samples within communities as well. At Taylors Mistake, *P. affinis* was the primary contributor to the between sample value ($\sum \overline{Si}$ % = 66.7%) (Table 3.4), at Kaikoura it was the second most important ($\sum \overline{Si}$ % = 34.7%) (Table 3.3), but at the Culvert the prawn was only the fifth most important contributor to the index ($\sum \overline{Si}$ % = 2.6%) (Table 3.2).

Similarly, both *P. affinis* and the gammarids were primary contributors to the dissimilarities between communities. *P. affinis* was the greatest contributor (22.1%) to the dissimilarity between the communities at the Culvert and Taylors Mistake (Table 3.5). Gammarid amphipods were, at 21.8%, the second highest contributor to the dissimilarity index. Together, *P. affinis* and gammarids were responsible for 43.9% of the dissimilarity between the two communities at the two sites. The same situation prevailed in comparisons in the samples from the communities at Taylors Mistake and Kaikoura, in which *P. affinis* was responsible for 18.9% of the total dissimilarity index, and gammarids, 17.4% (Table 3.6). Together they were responsible for over a third (36.3%) of the level of dissimilarity between the samples from the two sites.

Gammarid amphipods were the primary contributor to the dissimilarity (20.2%) between the Culvert and Kaikoura community samples, but *Micrelenchus tenebrosus* was the secondary contributor (18.0%) followed by *P. affinis* (12.6%) (Table 3.7). Gammarid amphipods and *P. affinis* contributed 32.8% of dissimilarity, while all three were together responsible for half the index (50.8%).

Table 3.2 Similarity within-site samples at the Culvert (Average Similarity = 58.45) based on contributions from each species. List of species' contribution cut off at 95%. $\overline{Si}$ = average contribution of the *i*th species and SD(*Si*) = standard deviation of the average contribution of the *i*th species.

Sp. Name	$\overline{Si}$	SD(S_i)	$\overline{Si}$ /SD(S_i)	$\Sigma\ \overline{Si}$ %
Paracalliope novizelandiae	32.39	13.61	2.38	55.41
Micrelenchus tenebrosus	13.31	13.18	1.01	22.77
Halicarcinus varius	3.38	2.30	1.47	5.78
Hemigrapsus crenulatus	2.51	1.65	1.52	4.30
Diadumene neozelandica	2.39	2.01	1.19	4.09
Palaemon affinis	1.49	2.71	0.55	2.55

Table 3.3 Similarity within-site samples at Kaikoura (Average Similarity = 37.61) based on contributions from each species. List of species' contribution cut off at 95%. $\overline{Si}$ = average contribution of the *i*th species and SD(*Si*) = standard deviation of the average contribution of the *i*th species.

Sp. Name	$\overline{Si}$	SD(S_i)	$\overline{Si}$ /SD(S_i)	$\Sigma\ \overline{Si}$ %
Gammaridae	15.86	11.17	1.42	42.18
Palaemon affinis	13.04	6.46	2.02	34.67
Sphaeromatidae	2.27	2.01	1.13	6.02
Cominella glandiformis	2.16	2.27	0.95	5.73
Melagraphia aethiops	1.89	3.10	0.61	5.04
Halicarcinus varius	1.28	2.72	0.47	3.40

Table 3.4 Similarity within-site samples at Taylors Mistake (Average Similarity = 33.37) based on contributions from each species. List of species' contribution cut off at 95%. $\overline{Si}$ = average contribution of the *i*th species and SD(*Si*) = standard deviation of the average contribution of the *i*th species.

Sp. Name	$\overline{Si}$	SD(S_i)	$\overline{Si}$ /SD(S_i)	$\Sigma\ \overline{Si}$ %
Palaemon affinis	22.26	24.46	0.91	66.71
Turbo smaragdus	3.78	9.22	0.41	11.33
Gammaridae	3.33	8.12	0.41	9.99
Petrolisthes elongatus	1.37	3.34	0.41	4.10
Pagurus novizealandiae	1.34	3.26	0.41	4.01

Table 3.5 Dissimilarity between the Culvert and Taylors Mistake hyperbenthic community samples (Average dissimilarity=79.77). $\overline{\delta}_i$ = average contribution from the *i*th species to the overall dissimilarity between all species pairs from each population and SD(δ_i) = standard deviation of the average dissimilarity.

Sp. Name	$\overline{\delta}_i$	SD(δ_i)	$\overline{\delta}_i$ / SD(δ_i)	$\Sigma\overline{\delta}_i$ %
Palaemon affinis	17.61	9.84	1.79	22.08
Gammaridae	17.38	11.43	1.52	21.79
Micrelenchus tenebrosus	12.27	8.64	1.42	15.38
Turbo smaragdus	5.96	6.08	0.98	7.47
Petrolisthes elongatus	4.61	5.99	0.77	5.78
Pagurus novizealandiae	4.59	5.96	0.77	5.75
Halicarcinus varius	2.52	1.79	1.41	3.16
Hemigrapsus crenulatus	2.19	1.44	1.52	2.75
Notoacmea helmsi	1.99	1.99	1.00	2.50
Diadumene neozelandica	1.97	1.17	1.68	2.47
Saccocirridae	1.94	3.29	0.59	2.43
Melagraphia aethiops	1.52	1.54	0.99	1.90
Armandia maculata	0.93	0.77	1.21	1.17
Macrophthalmus hirtipes	0.64	0.55	1.16	0.81

Table 3.6 Dissimilarity between the Taylors and Kaikoura hyperbenthic community samples (Average dissimilarity = 70.64). $\overline{\delta}_i$ = average contribution from the *i*th species to the overall dissimilarity between all species pairs from each population and SD(δ_i)= standard deviation of the average dissimilarity.

Sp. Name	$\overline{\delta}_i$	SD(δ_i)	$\overline{\delta}_i$/ SD(δ_i)	$\Sigma\overline{\delta}_i$%
Palaemon affinis	13.34	7.10	1.88	18.89
Gammaridae	12.30	8.98	1.37	17.42
Turbo smaragdus	5.96	6.14	0.97	8.44
Petrolisthes elongatus	4.61	5.99	0.77	6.52
Pagurus novizealandiae	4.59	6.04	0.76	6.49
Cominella glandiformis	3.57	4.15	0.86	5.05
Melagraphia aethiops	3.48	3.41	1.02	4.92
Halicarcinus varius	2.84	3.19	0.89	4.02
Tethya aurantium	2.07	4.22	0.49	2.93
Notoacmea helmsi	1.97	2.35	0.84	2.79
Polydora sp.	1.91	3.90	0.49	2.71
Saccocirridae	1.89	3.38	0.56	2.68
Sphaeromatidae	1.81	1.05	1.72	2.56
Scolecolepides benhami	1.62	3.31	0.49	2.29
Zeacumantus subcarinatus	1.51	1.61	0.94	2.14
Nodilittorina antipodum	1.44	2.94	0.49	2.03
Haploscoloplos cylindrifer	1.03	2.10	0.49	1.46
Capitellidae	0.73	11.06	0.66	1.03
Cirratulidae	0.70	1.43	0.49	1.00

Table 3.7 Dissimilarity between the Culvert and Kaikoura hyperbenthic community samples (Average dissimilarity = 68.29). $\overline{\delta}_i$ = average contribution from the *i*th species to the overall dissimilarity between all species pairs from each population and SD(δ_i)= standard deviation of the average dissimilarity.

Sp. Name	$\overline{\delta}_i$	SD(δ_i)	$\overline{\delta}_i$/ SD(δ_i)	$\Sigma\overline{\delta}_i$%
Gammaridae	13.80	9.72	1.42	20.21
Micrelenchus tenebrosus	12.27	1.59	1.43	17.97
Palaemon affinis	8.62	6.48	1.33	12.63
Cominella glandiformis	3.56	4.14	0.86	5.21
Melagraphia aethiops	3.38	4.02	0.84	4.95
Halicarcinus varius	3.14	2.21	1.42	4.60
Hemigrapsus crenulatus	2.19	1.44	1.52	3.21
Tethya aurantium	2.07	4.22	0.49	3.03
Diadumene neozelandica	1.97	1.17	1.68	2.89
Polydora sp.	1.96	3.84	0.51	2.86
Sphaeromatidae	1.81	1.04	1.74	2.65
Scolecolepides benhami	1.63	3.26	0.50	2.38
Zeacumantus subcarinatus	1.49	1.52	0.98	2.18
Nodilittorina antipodum	1.44	2.94	0.49	2.10
Haploscoloplos cylindrifer	1.07	2.06	0.52	1.57
Notoacmea helmsi	0.90	0.76	1.18	1.33
Armandia maculata	0.87	0.80	1.09	1.27
Cirratulidae	0.74	1.40	0.53	1.08
Capitellidae	0.65	1.14	0.57	0.95
Macrophthalmus hirtipes	0.64	0.55	1.17	0.94
Amphiura hinemoa	0.55	0.87	0.63	0.81
Austrovenus stutchburyi	0.42	0.37	1.15	0.62

There was a greater level of similarity between the samples from rock pools than those samples from the estuary (Culvert). For example, cluster analysis using Bray-Curtis similarity indices grouped Taylors Mistake sample t2 (April-May) with Kaikoura sample k4 (August-September) (49.9% similarity) (Fig. 3.1). In addition, sample t2 (April-May) from Taylors Mistake clustered with all the Kaikoura samples (k2, k3, k4, k5, k6) at a similarity level of ≥37.4% (Fig. 3.1, 3.2). This level of similarity between t2 and the entire Kaikoura sample series was slightly greater than that found at the Culvert and any rock pool sample. The Culvert samples (c1, c2, c3, c4, c5, c6) were 35.0% similar to sample t6 from Taylors Mistake (December-January). The Culvert and Kaikoura samples were less similar and all the Culvert samples were 31.1% similar to all Kaikoura samples.

Differences in levels of similarity between Taylors Mistake and Kaikoura were apparent in the MDS analysis, but not with cluster analysis. With MDS, the sample t2 (April-May, autumn) from Taylors Mistake was most similar to sample k3 (June-July, early winter) from Kaikoura (Fig. 3.2). Sample t2 clustered with k4 (August-September) at 49.9%, and was slightly less similar (45.5%) to sample k3 (Fig. 3.1).

3.3.1.2.The benthic community

All the benthic community samples were more than 15% similar using the same index (Fig. 3.4). As with the hyperbenthic communities, samples from the same sites were, as expected, generally more similar to each other, than they were to samples from the different sites. Again, as with the hyperbenthic samples, the benthic community samples from the Culvert were the most homogenous (64.7-76.1% similar, against 48.5-59.5% for Taylors Mistake, and 29.9-59.3% for the Kaikoura samples) (Fig. 3.4).

Species commonly collected in core samples from the Culvert were the cockle *Austrovenus stutchburyi*, the bivalve *Tellina liliana*, and numerous polychaetes, including *Aonides trifidus*, *Heteromastus filiformis*, *Prionospio pinnata*, and *Haploscoloplos cylindrifer*.

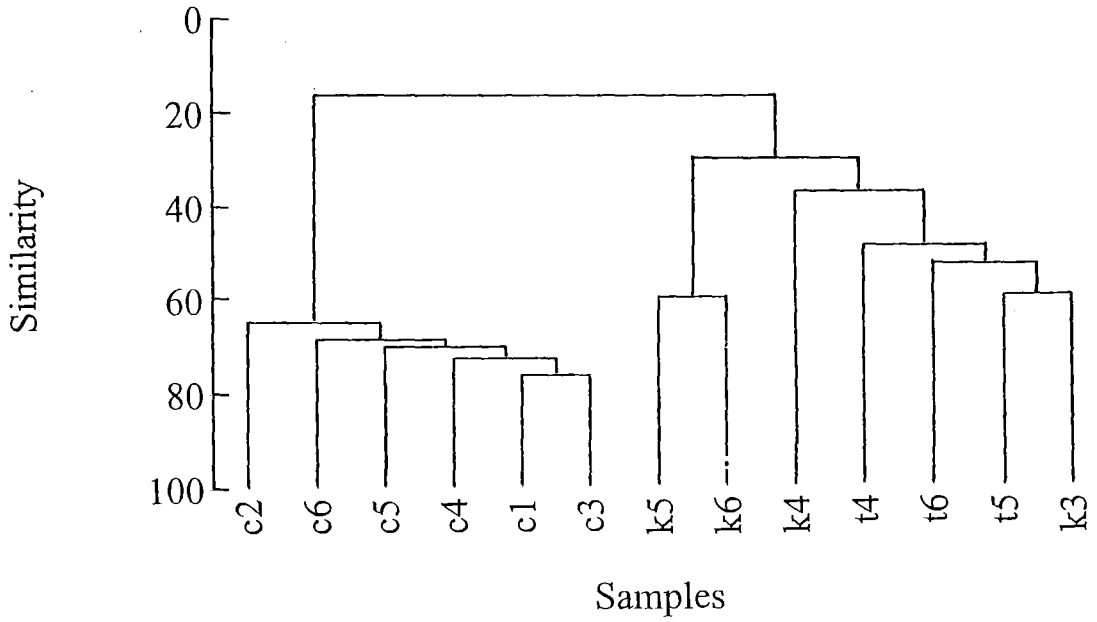


Fig. 3.4 Group-average clustering from Bray-Curtis similarities of benthic samples collected from the Culvert, Taylors Mistake, and Kaikoura in 2000. Culvert – c1, February-March; c2, April-May; c3, June-July; c4, August-September; c5, October-November; c6, December-January. Taylors Mistake – t2, April-May; t4, August-September; t5, October-November; t6, December-January. Kaikoura – k2, April-May; k3, June-July; k4, August-September; k5, October-November; k6, December-January.

At Taylors Mistake the common benthic species included the topshell *Melagraphia aethiops*, the catseye *Turbo smaragdus*, the periwinkle *Nodilittorina antipodum*, an amphipod (Gammaridae), an isopod (Sphaeromatidae), and a brittle star *Amphiura hinemoa*. As with Taylors Mistake, *Melagraphia aethiops* was common in benthic samples from Kaikoura, as were the bivalve *Protothaca crassicosta*, several polychaetes such as *Haploscoloplos cylindrifer* and *Polydora* sp., and the crab *Halicarcinus varius*.

No seasonal patterns in the similarity between the samples within a community were apparent in the cluster analysis. Spring and summer samples were most similar at Kaikoura (59.3%) (k5 and k6, October to January) as they were at Taylors Mistake – 52.7% for samples t5 (October-November) and t6 (December-January) (Fig. 3.4). The pattern was different in the Culvert samples in which the closest resemblances were between the late summer sample c1 (February-March) and winter sample c3 (June-July).

Similarities measured by MDS analysis differed from the cluster analysis for the samples from Kaikoura. There, the late winter to summer samples, k4, k5, and k6 (August to January) were more similar to each other than any was to the winter sample k3 (June-July) (Fig. 3.5). In contrast, cluster analysis grouped the spring and summer samples, k5 and k6 (October to January), and were only 29.9% similar to the k4 sample, as well as to k3 (Fig. 3.4).

As expected, and as found with the hyperbenthic communities, benthic communities from the rock pool sites were more similar to each other than either community was to the estuarine community. The October-November sample from Taylors Mistake (t5) and the June-July sample from Kaikoura (k3) were the most similar (at 59.5%) (Fig. 3.4), which was also greater than any similarity between the Taylors Mistake samples themselves. The greatest similarity between any Culvert sample and rock pool samples was only 15.9%, which was also the least level of similarity found between all samples.

In summary, the multivariate analysis confirmed the basic differences that exist between the communities occupying such different habitats as estuarine shell beds and mud in a tidal area continuously open to the sea and those on hard substrata that are periodically isolated from the sea and subjected to greater ranges of

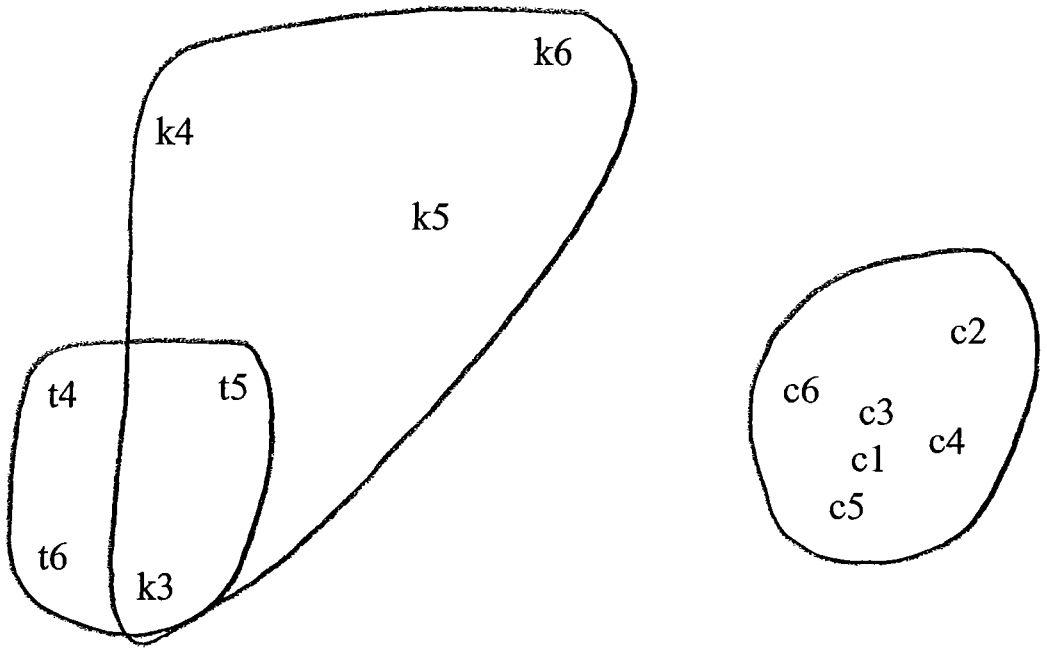


Fig. 3.5 MDS plot for benthic samples from the Culvert, Taylors Mistake, and Kaikoura collected in 2000. Culvert – c1, February-March; c2, April-May; c3, June-July; c4, August-September; c5, October-November; c6, December-January. Taylors Mistake – t2, April-May; t4, August-September; t5, October-November; t6, December-January. Kaikoura – k2, April-May; k3, June-July; k4, August-September; k5, October-November; k6, December-January.

temperature and to wave action. The results also demonstrate the differences between the rock pool sites along an open coast. Despite these differences, *Palaemon affinis* was a conspicuous, if not always abundant, member of all of them at most seasons.

3.3.1.3.Environmental factors

The environmental variables (minimum and maximum water depth, water temperature, type of substratum, the size of the rock pool or channel, and salinity) determined during each sampling were compared to determine which factors best matched the pattern in the communities.

Not surprisingly, samples from the rock pools were more similar to each other than any was to the estuarine samples, based on environmental data (Fig. 3.6, 3.7). For example, samples within populations tended to cluster together, with samples from Kaikoura grouping at distances of 3.0-1.2, those from the Culvert at 3.4-0.1, and those from Taylors Mistake at 4.1-0.8 (Fig. 3.6).

Samples within communities varied seasonally. For example, at the Culvert, the winter samples, c3 and c4 (June-September) clustered closely (distance 0.1; Fig 3.6). Summer samples, c1 and c6 (December-March) were also similar (distance 1.6). Winter samples (c3 and c4) were most similar to the autumn (April-May) sample, c2 (distance 2.9), and the summer samples were most similar to the spring sample c5 (October-November) (distance 2.1).

Data were not collected for all seasons at either Taylors Mistake or Kaikoura, so seasonal patterns were more difficult to discern. At Taylors Mistake, the autumn (April-May) sample, t2, and late winter (August-September) sample, t4, were most similar (distance 0.3; Fig. 3.6). Similarity between the spring (October-November) sample, t5, and early summer (December-January) sample, t6, was also high, with distance values of only 0.8. At Kaikoura, seasonal patterns were not apparent. The autumn sample, k2 (April-May) was most similar to the late winter sample, k4 (August-September) (distance 1.2). The spring sample, k5 (October-November) was also – again not surprisingly – more similar to the winter sample, k3 (distance 2.7), than to the late autumn and late winter samples, k2 and k4 (distance 3.0), which suggests that the variation being detected was not fundamental to the community composition but possibly was related to sampling biases.

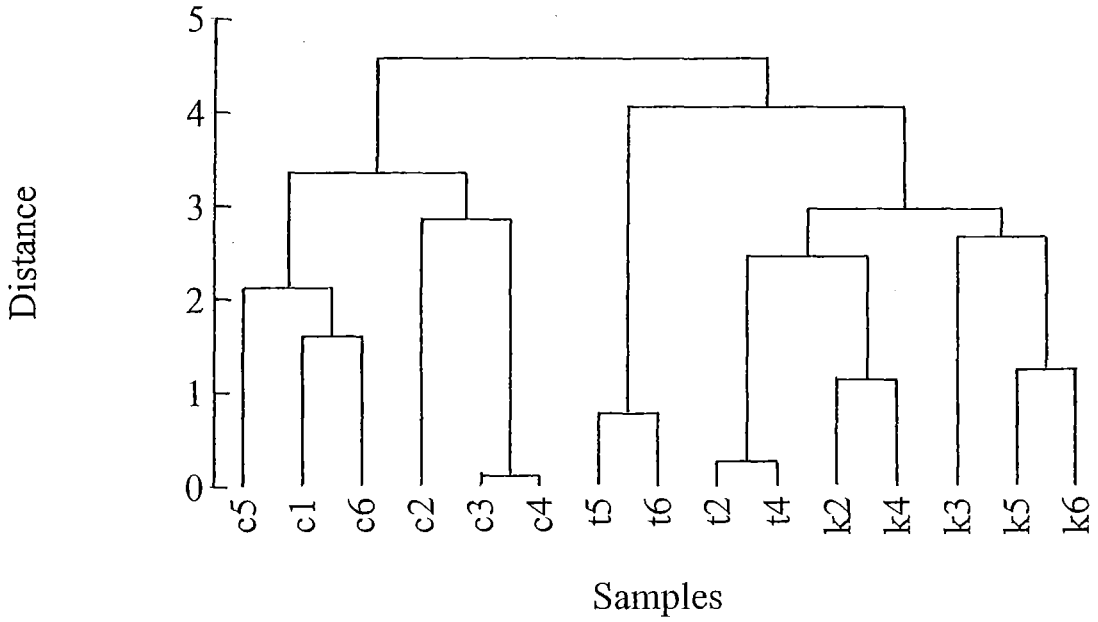


Fig. 3.6 Group-average clustering from Bray-Curtis similarities of environmental variables measured during sampling at the Culvert, Taylors Mistake, and Kaikoura in 2000. Culvert – c1, February-March; c2, April-May; c3, June-July; c4, August-September; c5, October-November; c6, December-January. Taylors Mistake – t2, April-May; t4, August-September; t5, October-November; t6, December-January. Kaikoura – k2, April-May; k3, June-July; k4, August-September; k5, October-November; k6, December-January.

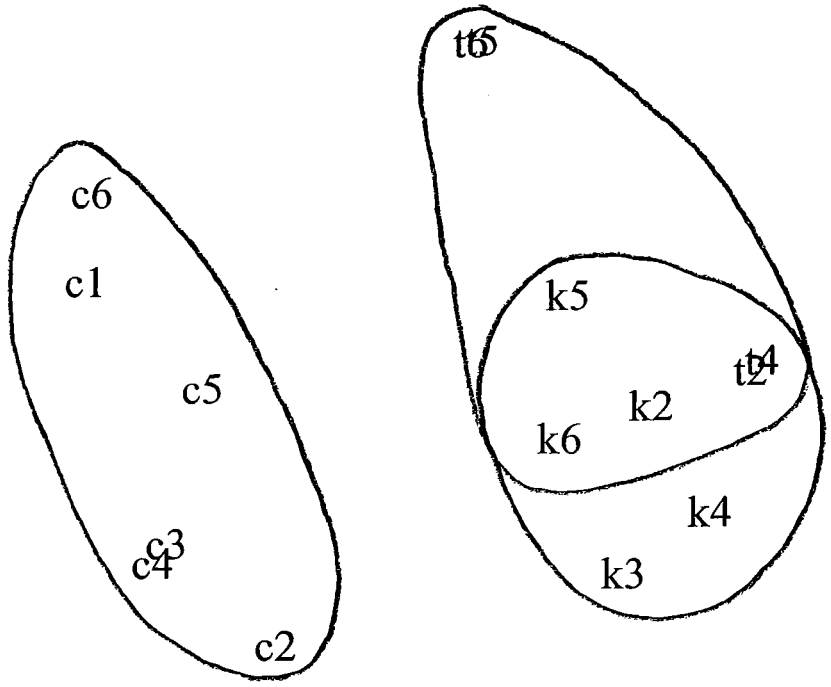


Fig. 3.7 MDS plot for environmental variables measured at the Culvert, Taylors Mistake, and Kaikoura during sampling in 2000. Culvert – c1, February-March; c2, April-May; c3, June-July; c4, August-September; c5, October-November; c6, December-January. Taylors Mistake – t2, April-May; t4, August-September; t5, October-November; t6, December-January. Kaikoura – k2, April-May; k3, June-July; k4, August-September; k5, October-November; k6, December-January.

Again, samples from the rock pools were more similar to each other than any were to the estuarine samples. Samples from Kaikoura and Taylors Mistake, excluding t5 and t6 from Taylors Mistake, were the most similar (distance 3.0; Fig. 3.6, 3.7). The distance between the two sets of rock pool samples was still less than the distance value of 4.6 found between the Culvert and any rock pool sample.

Using the BIO-ENV application in PRIMER®, environmental data collected during each sampling were compared to the patterns in the hyperbenthic community samples to determine which variables best matched the differences observed between the communities. Within populations, minimum water depth, maximum water depth, water temperature, and salinity were not highly correlated with the community pattern, except at Taylors Mistake (Table 3.8). There, salinity changes through the year were responsible for ~ 89% of the similarity between the samples (r = 0.886), but none of the other environmental variables matched the pattern in the community (r values $\leq$ 0.143). The environmental variables were not good predictors of the composition of the hyperbenthic community samples from the Culvert or Kaikoura (no correlation value > 0.281; Table 3.9, 3.10).

Table 3.8 Combination of 4 environmental variables (minimum water depth, maximum water depth, water temperature, and salinity), taken k at a time, yielding the best environmental variable matching the hyperbenthic community sample matrix at Taylors Mistake for each k. Bold type indicates the overall optimum match.

k	Best variable combinations (ρ_w)
1	**Salinity (r=0.886)**
2	Salinity, Minimum Water Depth (r=0.143)
3	Salinity, Maximum Water Depth (r=0.143)
4	Salinity, Minimum Water Depth, Maximum Water Depth (r=0.143)

Table 3.9 Combination of 4 environmental variables (minimum water depth, maximum water depth, water temperature, and salinity), taken *k* at a time, yielding the best environmental variable matching the hyperbenthic community sample matrix at the Culvert for each *k*. Bold type indicates the overall optimum match.

k	Best variable combinations (ρ_w)
1	**Water Temperature (*r*=0.061)**
2	Salinity (*r*=0.021)
3	No variables (*r*=0.000)
4	Salinity, Water Temperature (*r*= -0.014)

Table 3.10 Combination of 4 environmental variables (minimum water depth, maximum water depth, water temperature, and salinity), taken *k* at a time, yielding the best environmental variable matching the hyperbenthic community sample matrix at Kaikoura for each *k*. Bold type indicates the overall optimum match.

k	Best variable combinations (ρ_w)
1	**Maximum Water Depth (*r*=0.281)**
2	Maximum Water Depth, Salinity (*r*=0.055)
3	Salinity (*r*=0.024)
4	No variables (*r*=0.000)

Between communities, the combination of gravel, rock or mud, minimum water depth, and water temperature provided the best indications of similarity between the communities (r = 0.539) (Table 3.11). Gravel, which was present at Kaikoura alone, was responsible for ~ 40% of the similarity between the variables and the community samples (r = 0.405). The presence or absence of rock or mud provided the next best match, adding an additional ~ 11% similarity (r = 0.512). Even though there was rock rubble along the shoreline of McCormacks Bay, there was no rock in the substratum of the Culvert channel, so rock was present only at the rock pool sites. The addition of minimum water depth and water temperature added little to the predictive value of the environmental variables (3%; r = 0.539). The range of minimum water depth was lower at the rock pool sites (Kaikoura varied by 5-15 mm; Taylors 5-18 mm), whereas the Culvert minimum water depth varied by 10-30 mm. Peak water temperature was lower at Kaikoura (7-20°C) and the Culvert (9.5-22°C), than at Taylors Mistake (7-25°C), but the latter had a broader range.

3.3.2. Natural food preferences of *Palaemon affinis*

3.3.2.1.General

Of the total of 264 prawn stomachs examined in the study, only 28.8% were ≥50% full, but the proportion differed between populations. A greater percentage (39.1%) of 69 stomachs from Taylors Mistake and 32.6% of 95 stomachs from the Culvert were ≥50% full, but only 18.0% of 100 stomachs from Kaikoura were ≥50% full.

The stomach contents of wild-caught *P. affinis* included a variety of food items, but amphipods were the most important component in the prawn's diet (P<0.001); 71.1% of stomachs that were ≥50% full contained pieces of amphipod. In addition, the proportion containing amphipods did not differ significantly between populations: Taylors Mistake, 77.7%; Culvert, 67.7%; Kaikoura 66.7% (Fig. 3.8). Unidentifiable matter (generally ascribable to muscle tissue, but not attributed to any taxon) and polychaetes, were the next most important components in the diet. Both categories were found in 14.5% of all stomachs. Other items, including plant material, gastropods, bivalves, ostracods, sponge spicules, sand grains and crab fragments, were found in some stomachs. Gastropods and bivalves were identified only in stomachs from prawns collected at Taylors Mistake (Fig. 3.8). The bivalves

Table 3.11 Combinations of 8 environmental variables (minimum water depth, maximum water depth, water temperature, rock, mud, gravel, size of pool or channel, and salinity), taken *k* at a time, yielding the best environmental variable matching the hyperbenthic community sample matrix for all sites for each *k*. Bold type indicates the overall optimum match.

k	Best variable combinations (ρ_w)
1	Gravel ($r = 0.405$)
2	Gravel, Rock or Mud ($r = 0.512$)
3	Gravel, Rock or Mud, Minimum Water ($r = 0.539$)
4	**Gravel, Rock or Mud, Minimum Water, Water Temperature** **($r = 0.539$)**
5	Gravel, Rock, Mud, Water Temperature ($r = 0.516$)

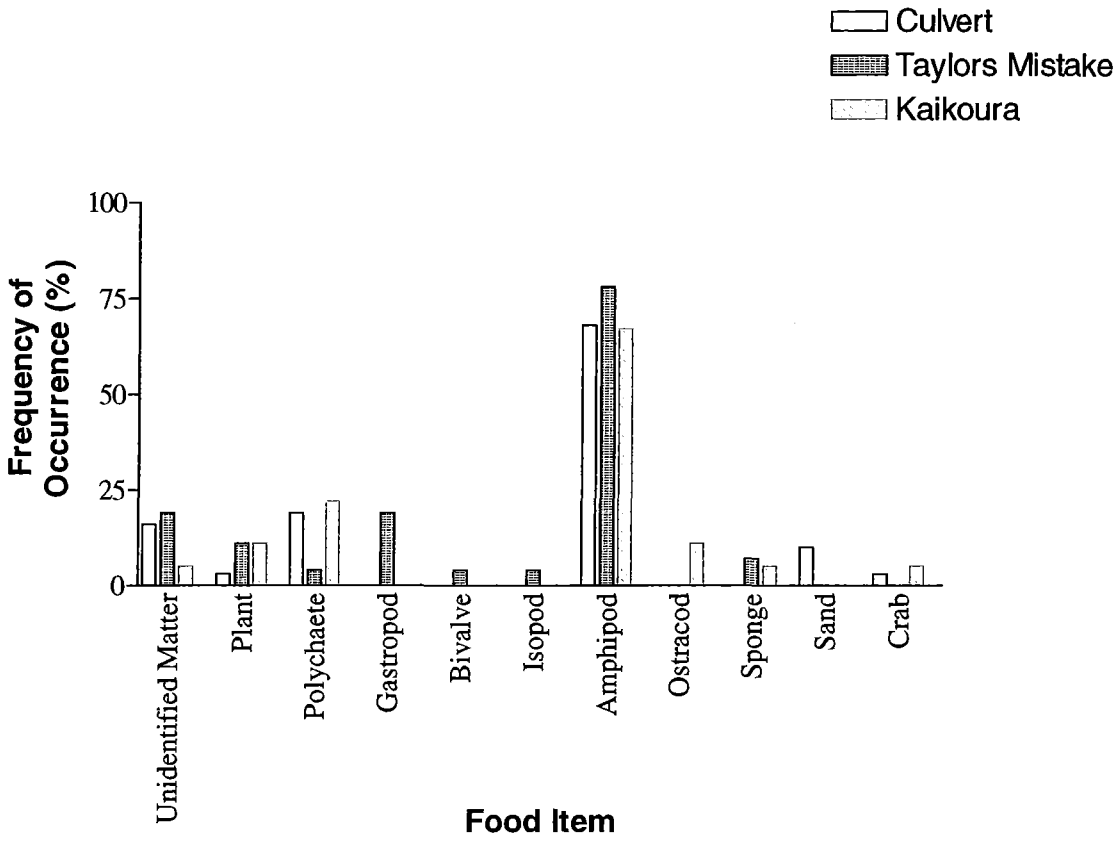


Fig. 3.8 Frequency (%) of occurrence of food items (by major taxon) found in stomachs of *Palaemon affinis* collected from the Culvert, Taylors Mistake, and Kaikoura in 2000. Percentage of frequency was determined by the number of stomachs containing food item *i*, divided by number of stomachs ≥50% full.

that had been consumed were typically small and eaten whole, but the size of gastropods recorded in stomachs varied. Small topshells as well as operculae from much larger individuals were recorded. Sand grains and sponge spicules were recorded in a small percentage of stomachs (2.1% for both in all females and 7.1% for both in all males; Table 3.12) and were not present in stomachs from all sites. Only prawn stomachs from samples from the Culvert (9.7%) contained sand grains, whereas sponge spicules were found only in stomachs from Taylors Mistake (7.4%) and Kaikoura (5.6%) (Fig. 3.8). Both sand grains and sponge spicules were closely associated with pieces of amphipod and may have been ingested at the same time, and could have been part of the stomach contents of the amphipods themselves.

3.3.2.2.Sex differences in choice and amount of food

No significant differences were found in the food preferences between male and female *P. affinis* within or between any of the populations or for the pooled samples from the three sites. Male and female prawns consumed similar food items, and amphipods were apparently the primary food of both sexes (in 68.8% of females and 75.0% of males, $P>0.05$) (Table 3.12). Similar proportions were found in male and female prawns in the individual populations. As noted above, other organisms were consumed, but they did not contribute significantly to either sex's diet.

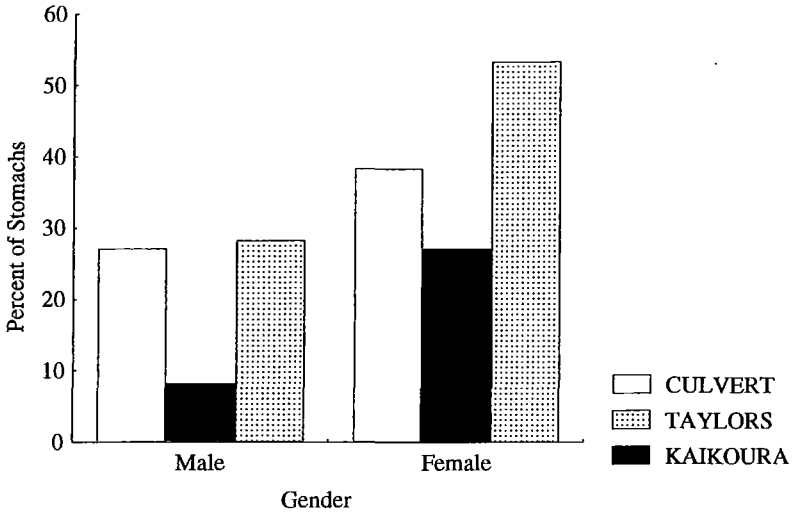
The stomach content of individual prawns below the minimum externally sexable size of males (MESS; Culvert, ≥9 mm CL (n=9); Taylors Mistake ≥8 mm CL (n=3); and Kaikoura, ≥5 mm CL (n=0)) did not differ from adult *P. affinis*. Only two stomachs from individuals below the MESS from Taylors Mistake contained food remains: one was 100% full, containing a small topshell and pieces of amphipod; the second was ≥50% full and contained pieces of amphipod.

In contrast to the homogeneity of the diet, the amount of food consumed differed between the sexes. The proportion of females with ≥50% full stomachs was consistently higher than the males in each population (Fig. 3.9a). For example, 27.1% of all females from Kaikoura had ≥50% full stomachs, whereas the proportion of males with that level of fullness was only 8.2%. Similarly, a larger proportion of females from Taylors Mistake (53.3%) and the Culvert (38.3%) had ≥50% full stomachs than did the males (28.2% at Taylors Mistake, 27.1% at the Culvert).

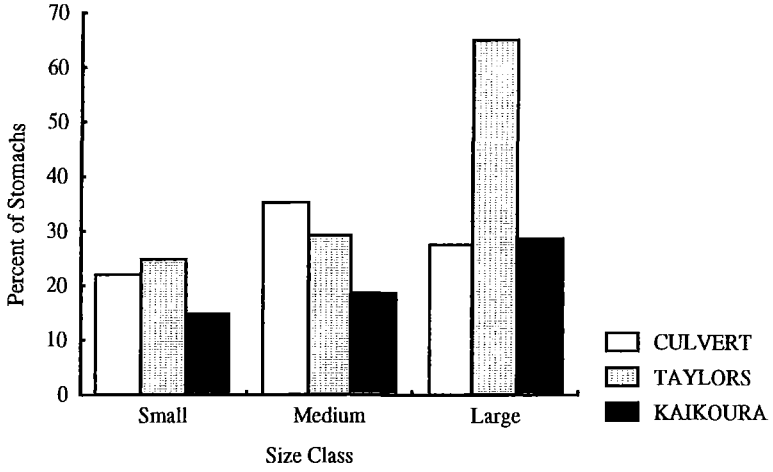
Table 3.12 Frequency (%) of occurrence of food items (by major taxon) found in stomachs of male and female *Palaemon affinis* collected from the three study sites: the Culvert, Taylors Mistake, and Kaikoura, and for all three sites pooled. Frequency of occurrence was determined from the number of stomachs containing food item *i*, divided by the number stomachs ≥50% full. Sample sizes for analysis of diet composition were: the Culvert 13 males, 18 females; Taylors Mistake 11 males, 16 females; Kaikoura, 4 males, 14 females; pooled data, 28 males, 48 females.

	% Frequency of Occurrence							
	Culvert		Taylors Mistake		Kaikoura		Pooled Data	
Diet	Males	Females	Males	Females	Males	Females	Males	Females
Unidentified matter	7.7	22.2	9.1	25.0	0.0	7.1	7.1	18.8
Plant material	7.7	0.0	18.2	6.3	0.0	14.3	10.7	6.3
Polychaete	38.5	5.6	9.1	0.0	25.0	21.4	25.0	6.3
Gastropod	0.0	0.0	18.2	18.8	0.0	0.0	7.1	6.3
Bivalve	0.0	0.0	0.0	6.3	0.0	0.0	0.0	2.1
Isopod	0.0	0.0	0.0	6.3	0.0	0.0	0.0	2.1
Amphipod	61.5	72.2	90.9	68.8	75.0	64.3	75.0	68.8
Ostracod	0.0	0.0	0.0	0.0	0.0	14.3	0.0	4.2
Sponge spicules	0.0	0.0	9.1	6.3	25.0	0.0	7.1	2.1
Sand grains	15.4	5.6	0.0	0.0	0.0	0.0	7.1	2.1
Crab	0.0	5.6	0.0	0.0	0.0	7.1	0.0	4.2

a)



b)



c)

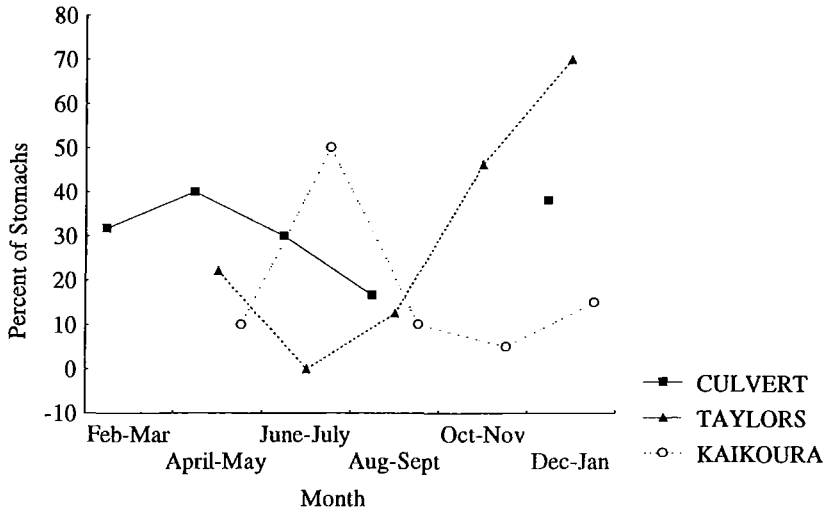


Fig. 3.9 The percent of stomachs of *Palaemon affinis* ≥50% full by: a, sex; b, size class; and c, season, for prawns collected from the Culvert, Taylors Mistake, and Kaikoura in 2000..

Additionally, a high proportion of ovigerous females from rock pools had ≥50% full stomachs (all ovigerous females from Taylors Mistake (n=7) and Kaikoura (n=1) had ≥50% full stomachs, as against 22.2% of females from the Culvert).

3.3.2.3.Food preferences by size class

No significant differences were found between the food preferences of any of the 2 mm size classes within or between any population(s), or in the pooled data. The most common food item in all size classes was amphipods, and at least 50% of all stomachs in each class size at each site contained amphipod pieces (Fig. 3.10).

Size class parameters in relation to growth determined for each population were described in Chapter Two, Section 2.4.2. To compare growth with food consumption, the percent fullness of stomachs was compared for the three size classes (Culvert and Taylors Mistake, small 5-8 mm CL, medium 9-14 mm CL, large 15-21 mm CL; Kaikoura, small 5-8 mm CL, medium 9-12 mm CL, large 13-15 mm CL). No pattern in percentage fullness was found between the sites for the different sizes (Fig. 3.9b). At Taylors Mistake and Kaikoura, the percentage fullness increased with increasing size class, for example, at Taylors Mistake 25.0% of the small size class had ≥50% fullness, 29.3% of the medium, and 65.0% of the large. However, at the Culvert, the largest percent fullness, 35.3%, was observed in the medium size class, with 22.2% of the small and 27.8% of the large having guts ≥50% full.

3.3.2.4.Seasonal patterns in diet and food consumption

The content of food material recorded in *P. affinis* stomachs did not change throughout the year, hence the food preferences were apparently the same: amphipods were the main food item regardless of season. In all months that stomach content data was available (in some months no *P. affinis* were collected from a particular site), at least 50.0% of all stomachs contained amphipod pieces (Fig. 3.11).

In addition, no seasonal patterns in percent fullness were found (Fig. 3.9c). Although low proportions (10.0-16.6%) of ≥50% full stomachs were found at all sites in August-September, this did not represent a trend. In April-May at Kaikoura, 10.0% of the stomachs from that sampling period were ≥50% full, increasing to a peak 50.0% of stomachs in June-July, but the proportions then declined dramatically to

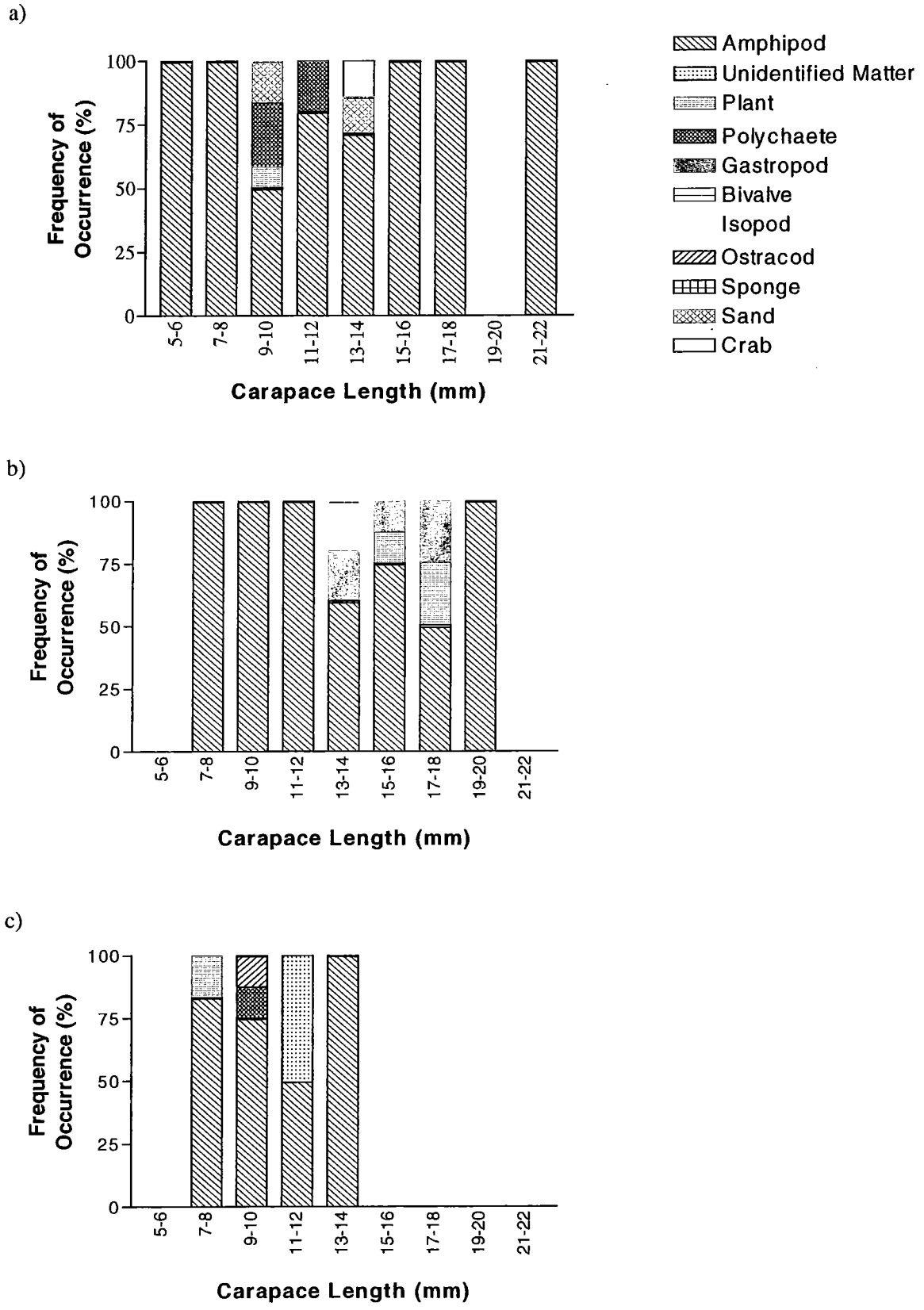
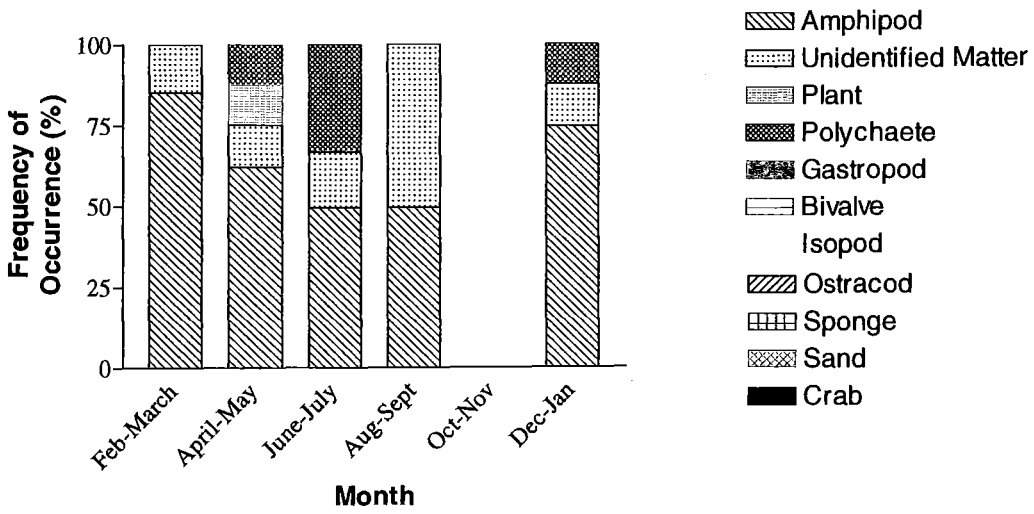
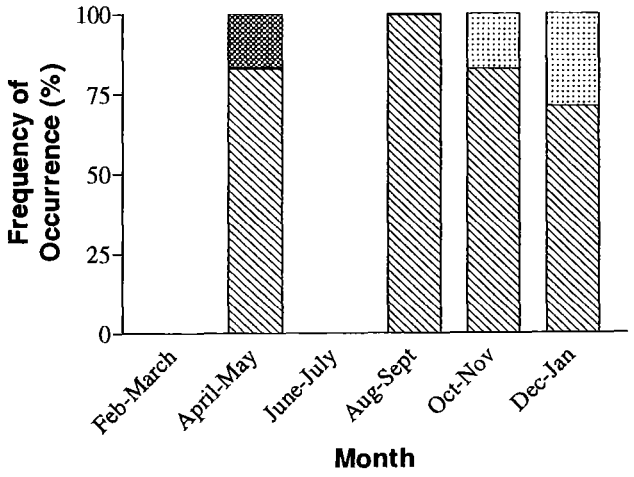


Fig. 3.10 Frequency (%) of occurrence of food items (by major taxon) found in stomachs of *Palaemon affinis* (by 2 mm size classes) collected from: a, the Culvert; b, Taylors Mistake; and c, Kaikoura in 2000.

a)



b)



c)

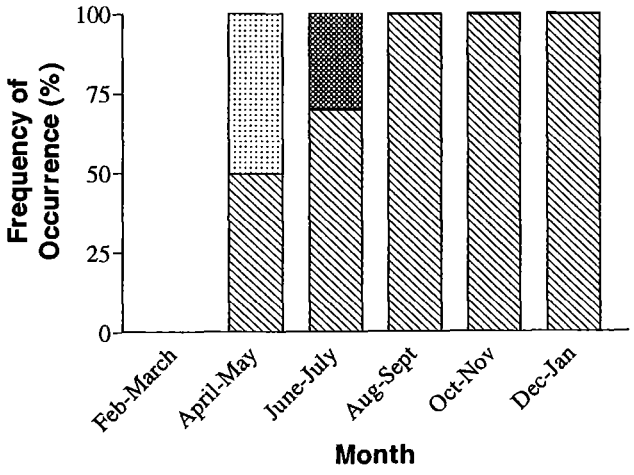


Fig. 3.11 Frequency (%) of occurrence of food items (by major taxon) found in stomachs of *Palaemon affinis* collected bimonthly from: a, the Culvert; b, Taylors Mistake; and c, Kaikoura in 2000.

10.0% in August-September, and continued to decline to 5.0% in October-November. This pattern in percent fullness differed from that observed at Taylors Mistake and the Culvert. When the proportion of full stomachs was low at Kaikoura (15.0%) in December-January, the proportion of full stomachs peaked at Taylors Mistake (70.0%). Similarly, peak levels of percentage fullness were observed at the Culvert (40.0% in April-May), when the proportion was low at both Kaikoura (10.0%) and Taylors Mistake (22.2%).

3.4. Discussion

3.4.1. The "*Palaemon affinis* community" in different habitats

The presence of gammarid amphipods may be one of the most important factors influencing the occurrence of *Palaemon affinis* in the intertidal communities investigated in this study. The *P. affinis* communities from the Culvert, Taylors Mistake, and Kaikoura contained few species in common. Species composition at different seasons was consistently dominated by gammarid amphipods suggesting that gammarid amphipods are the most common link between samples within each site through time. Gammarid amphipods are the most common animal group in the estuary and rock pools that differ substantially as habitats, both physical and biotic. Gammarid amphipods were the most important food component in the natural diet of *P. affinis*. If *P. affinis* relied upon gammarid amphipods as their main food source, the distribution of that prey could in part determine the distribution of *P. affinis*. Distribution resulting from prey movements has been suggested for *Palaemon macrodactylus* (Sitts & Knight 1979). Sitts & Knight (1979) suggested that the daily distribution of *P. macrodactylus* might be determined, in part, by its primary prey, the mysid *Neomysis mercedis*.

Within each community the composition appeared to be largely unrelated to the environmental factors that were measured in this study. However, at Taylors Mistake salinity was significantly correlated with the community composition. Kirkpatrick (1981) and Kirkpatrick & Jones (1985) reported high survival of *P. affinis* in a wide range of salinities (5-43‰), which suggests that salinity does not directly affect the distribution of *P. affinis*. In contrast, environmental factors have been suggested to affect the distribution of other *Palaemon* species. For example, Bamber

& Henderson (1994) suggest that adult *Palaemon serratus* migrate from the upper Severn Estuary to the sea to avoid lower winter salinities, while the migration of *P. serratus* from the Thames Estuary appeared to correspond with minima water at summer (Attrill & Thomas 1996), but neither has been confirmed.

Gammarid amphipods and *P. affinis* were good discriminating species between the communities; they not only contribute much to the dissimilarity between the populations, but they also consistently dominate the similarity comparisons of all samples in the two populations. The fluctuations in abundance of both groups varied between the sites, but gammarid amphipods varied much more than *P. affinis*. The numbers of amphipods differed between the habitats, with the greatest numbers occurring at the Culvert.

Because gammarid amphipods and environmental variables most reflect the differences between the rock pool and estuarine habitats, environmental variables may potentially be responsible for limiting the distribution of gammarid amphipods. If the distribution of *P. affinis* was also, at least in part, determined by the distribution of the amphipods, then that would further support the apparently close (trophic level) relationship between gammarid amphipods and *P. affinis* within the community structure, i.e., the prawn depends on the amphipods as its primary food source. However, as many factors influence the community composition and structure, using the present data it is difficult to determine which factors control the community composition. Experiments entailing the manipulation of single variables and observing the effects on community composition would be necessary to test the inter-related effects of the physical and biotic environments. In particular, further research on the environmental requirements of the gammarid amphipods, *P. affinis*, and their interactions is needed before a causal relationship between the distributions of the two taxa could be confirmed.

3.4.2. Natural food preferences of *Palaemon affinis*

Compared with other *Palaemon* species, the proportion of food found within the stomachs of field collected *Palaemon affinis* was low, with only 29% of the prawn stomachs more than 50% full. Guerao (1995) reported 60% of *Palaemon xiphias* stomachs were more than 50% full, while Guerao & Ribera (1996) reported 70% for

P. serratus. Both Guerao (1995) and Guerao & Ribera (1996) preserved live animals in 70% alcohol in the field, whereas live animals in this study were killed and preserved in 10% formalin. Forster (1951) suggested that stomach content is lost when live animals are placed in formalin, which might explain the lower gut fullness in *P. affinis* than *P. xiphias* and *P. serratus*. However, in the present study, no prey remains were observed in the specimen containers and no animals were observed to eject food material. In addition, the proportion of stomachs with more than 50% fullness varied during the year, apparently without a consistent pattern. For example, 70% of all stomachs of prawns collected from Taylors Mistake in December-January were more than 50% full. If stomach content was lost during preservation, low proportions of relative fullness would be observed consistently in samples from all sites throughout the year. Nevertheless, further research is needed to determine if the proportion of full stomachs in samples of *P. affinis* is normally low or whether the low proportions observed here resulted from the expulsion of gut contents on immersion in formalin, or from the time of collection.

The results of this study show that *P. affinis* is mainly carnivorous, with amphipods as its main identifiable natural food. Also, personal observations of *P. affinis* capturing live prey suggests that *P. affinis* is more predatory than was once believed. Plant material, as well as sand particles, have been found in the stomach of this prawn and in other species of *Palaemon* (Subrahmanyam 1975; Sitts & Knight 1979; Guerao 1995; Guerao & Ribera 1996), but they generally constituted only a minor component in terms of frequency of occurrence. Plant material may have been accidentally ingested as *P. affinis* gleaned prey from amongst the algae. Amphipods were typically found in large numbers in the *Ulva* and *Corallina* dominated samples. It is interesting to note here that *Ulva* and *Corallina* may function both as a refuge for *P. affinis* from its predators and as the habitat of its own principal prey. However, it cannot be confirmed that the animal material found in *P. affinis* stomachs was from animals actually killed by the prawn. *P. affinis* has also been observed scavenging on carrion, including mussel and fish flesh. This is not surprising, as most predators, including lions and eagles, regularly include carrion in their diet. Sand particles in the stomach may have been ingested accidentally when *P. affinis* fed on dead animal material lying on the sediment. The observation that *P. affinis* can feed on both live

and dead animal material suggests that *P. affinis* is an opportunistic feeder, however, the abundance of gammarids in the diet suggests that it is an efficient predator with much of its energy intake obtained from live food.

Other species of *Palaemon* have been reported as being mainly carnivorous. The primary food component in the diet of *Palaemon xiphias* is amphipods, with plant material playing a minor role (Guerao 1995). Guerao (1995) further suggested that the presence of plant material in the stomach was the result of accidental ingestion when capturing prey from amongst algae. Similarly, *P. macrodactylus* fed primarily on animal material, mysids in particular, while plant material also played a lesser role (Sitts & Knight 1979). Sitts & Knight (1979) suggested the plant material found in the stomach might have originated in the guts of consumed prey. Neither author considered scavenging as an alternative feeding strategy.

Palaemon adspersus (Inyang 1978), *P. styliferus* (Subrahmanyam 1975) and *P. serratus* (Forster 1951) are reported to be omnivores, but crustaceans were an important food item in all stomach content when examined as percent frequency occurrence. 35.4% of *P. adspersus* stomachs contained amphipod pieces, which was the greatest contributor to the content: 37.51% of *P. styliferus* stomachs contained amphipod pieces (2nd greatest contributor) (Subrahmanyam 1975), while crustaceans were a significant proportion of *P. serratus* diet (Forster 1951).

The diet of *Palaemon* species may be related to food availability (Guerao & Ribera 1996). Guerao & Ribera (1996) and Forster (1951) have presented differing descriptions of the diet of *P. serratus*. Guerao & Ribera (1996) found *P. serratus* from the Spanish Mediterranean were mainly carnivorous, feeding primarily on gastropods and amphipods, with little plant material ingested. Conversely, Forster (1951) found *P. serratus* from Plymouth, UK to be omnivorous. Forster found both algae and small crustaceans were the primary food components in its diet. However, Forster specifically stated that algae was a considerable part of the diet from prawns collected inshore, but did not mention if algae was important in the prawns collected further offshore. Guerao & Ribera (1996) suggested the discrepancy in diet composition between the populations may be the related to food availability within each community. The secondary food items consumed by *P. affinis* in this study varied between the populations. For example, gastropods and bivalves were found in

the stomach content of prawns from Taylors Mistake, but not the Culvert or Kaikoura. Amphipod abundance at the Culvert was much higher than at Taylors Mistake, which may have offered *P. affinis* from the Culvert more opportunities to consume amphipods. This would support the suggestion that the diet of *Palaemon* is related to food availability. While food availability may determine the composition of the diet of *Palaemon* species, other variables, such as prey susceptibility and predator avoidance, may also be important. Further research on the feeding behaviour is needed to determine whether *P. affinis* is a predator.

Differences in natural food preferences were not found between male and female *P. affinis*, which is similar to other species of *Palaemon*. Male and female *P. xiphias* (Guerao 1995) and *P. serratus* (Guerao & Ribera 1996) have been reported as having similar food preferences.

Similarly, there was no difference in the natural food preferences of the different size classes of *P. affinis* in this study, which is similar to *Palaemon adspersus* (Inyang 1978). However, different size classes of *P. serratus* (Guerao & Ribera 1996) and *P. xiphias* (Guerao 1995) have been shown to have different food preferences. In both species, larger prawns consumed a wider range of prey. For example, Guerao (1995) reported that the frequency of occurrence of isopods, decapods, gastropods, and polycheates increased with size in *P. xiphias*, while the frequency of mysids and copepods decreased, but did not suggest a reason for the differences.

In addition, other studies on *Palaemon* have included analysis of the relationships between prey size and the size of the prawn. Guerao (1995) reported that the size and hardness of prey increased with prawn size in *Palaemon xiphias*. Similarly, prey size increased with size in *P. macrodactylus* (Sitts & Knight 1979), as it did also in *P. serratus* (Guerao & Ribera 1996). Furthermore, the frequency of mollusc remains in *P. xiphias* stomachs increased with the size of the prawn (Guearo 1995). The size and hardness of food items were not measured in this study, but *P. affinis* from Taylors Mistake as small as 21 mm total body length (TBL) were found to have consumed gastropods. In addition, the frequency of gastropods was greater in smaller *P. affinis* (21-46 mm TBL) than in larger prawns (46-50 mm TBL), which differs from the situation reported for *P. xiphias* (Guerao 1995).

Seasonal differences in the frequency of occurrence of food items were not found in *P. affinis* in this study, suggesting that abundance of their preferred prey, gammarid amphipods, remains constant. Comparisons cannot be made with other literature as no reports of seasonal patterns were given. Forster (1951) noted the diet of *Palaemon serratus* varied with the season, but not enough detail was provided for comparisons here. In this first study of community composition and feeding preferences of *P. affinis*, the results suggest that the distribution of *P. affinis* may be determined by the availability of preferred prey.

Chapter Four

Behaviour of *Palaemon affinis*

Chapter Four: Behaviour of *Palaemon affinis*

4.1. Introduction

To date there have been no descriptions of the behavioural patterns of *Palaemon affinis*. However, as circatidal and diel rhythms are reported to control the locomotor activity of many species in the genus *Palaemon* (Forster 1951; Jansson & Källander 1968; Rodriguez & Naylor 1972; Inyang 1978; Hagerman & Ostrup 1980; Fincham & Furlong 1984; Guerao 1995; Guerao & Ribera 1996), it is reasonable to assume that such factors are important in the biology of *P. affinis*. Additionally, several authors have suggested that *Palaemon* species might be nocturnal feeders (Inyang 1978; Guerao 1995; Guerao & Ribera 1996). This would affect the opportunity of the prawn to feed if the preferred food was available only at a particular state of the tide, which would be in daylight on at least half the days each month. Some information on the behavioural patterns of the prawn with respect to tidal and light:dark regimes is therefore necessary before ecological information can be properly interpreted.

As the behavioural repertoire of *P. affinis* is doubtlessly extensive and complex, the behavioural components of this study were limited to the effects of tidal and light cycles on locomotor and feeding activity, even though those activities may be influenced by many other variables. Locomotor activity was selected because it affects many aspects of the prawn's life, such as searching for food, migratory behaviour, and predator avoidance. It is also relatively straightforward to observe and quantify, in comparison to other behaviours. The results of the laboratory experiments described here for *P. affinis* provide a context for interpretation of the ecological data on food choice and choice of habitat.

Observations of the prawn behaviour in the field are difficult and would require specialised equipment and methodology and were outside the scope of the present study. It is likely, however, that specimens would retain elements of their behavioural patterns in the conditions of captivity, where the physical environment can be manipulated. For example, the spider *Desis marina* is believed to live below the high tide line in holdfasts of *Durvillaea antarctica* at Point Kean, Kaikoura. Under laboratory conditions it was found that *Desis marina* was capable of surviving

long periods of submergence (McQueen & McLay 1983), suggesting that the behavioural patterns of the spider persisted even under unnatural conditions.

Casual observations of other aspects of behaviour, such as prey handling, have been included where available because they shed light on the predatory ability of the prawn as inferred from the indirect information on stomach contents. Although the behaviours exhibited in the laboratory are less complex than the behavioural cues and releasers in the natural environment, captive experiments can provide basic data on the behavioural repertoire of most species, especially invertebrates.

4.2. Laboratory manipulations – activity in relation to tidal or light cycles

4.2.1. Experimental tide tank system

To examine the effects of tide and light cycles on locomotor and feeding activity, two tidal tank systems were set up in an enclosed room at the Edward Percival Field Station, Kaikoura, New Zealand (Plate 4.1). As no temperature control room was available for experiments, water temperature was maintained for individual experiments by using a continuous supply of fresh flowing seawater (for specific water temperatures, see experimental methods, Section 4.2.2). Each tidal tank system consisted of a reservoir tank, an experimental tank, and a pump.

The reservoir tank was a rectangular 0.0821 m^3 PVC tank with a single water inlet valve and a single water outlet valve. The reservoir tank was supplied continuously with fresh seawater from the laboratory supply. Within the reservoir, a water pump (Maxijet® MJ 250, 370 l/h), set by a timer to simulate the natural tide cycle at Kaikoura, supplied water to the experimental tank.

The experimental tank was a rectangular 0.0466 m^3 PVC tank with a single water inlet and two outlets arranged as vertical pipes of different heights. One of the outlets was 100 mm taller in the tank than the other and was 20 mm in diameter, whereas the shorter outlet had a diameter of 15 mm. When the pump was running, it supplied water to the tank faster than the shorter outlet could drain it, causing the water level in the tank, the "tide", to rise. Each change in tide took 10 minutes. The upper outlet prevented overflow and gave a constant depth at "full tide".

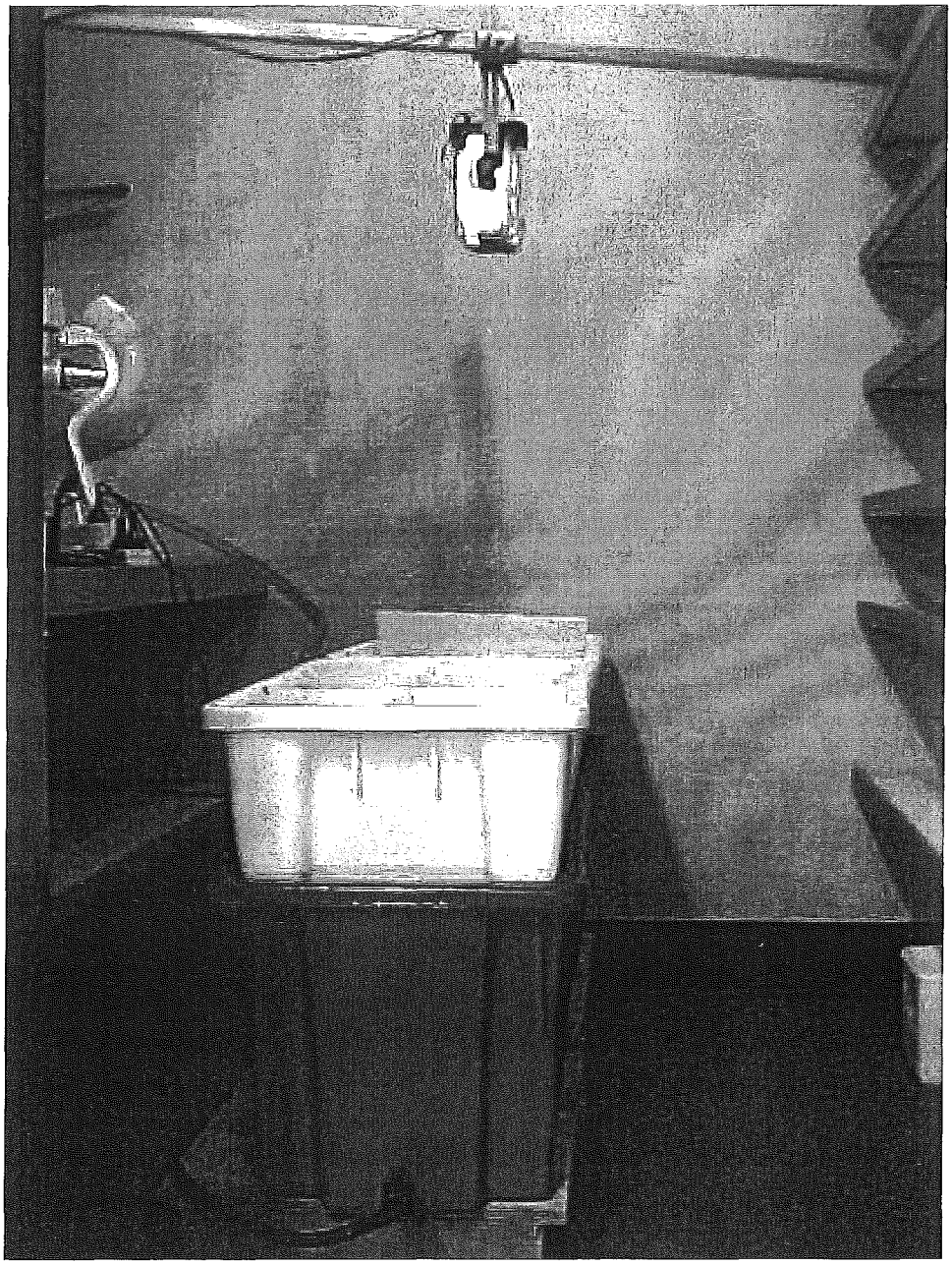


Plate 4.1 Tidal tank system in an enclosed room at the Edward Percival Field Station, Kaikoura, in 2000. The bottom reservoir tank was supplied continuously with fresh flowing seawater from the laboratory supply, which in return supplied water to the top experimental tank via a pump set to simulate the natural tide cycle at Kaikoura.

The experimental tank was divided into eight sections by flat sheets of opaque PVC (Plate 4.2). Three rows of 4.5 mm holes were drilled through the bottom of each partition to allow water to flow freely between the sections to maintain the level, and to restrict the prawns to separate compartments. A netting of 1.5 mm mesh was glued along the sides and bottom of the partitions as an additional measure to prevent prawns from moving between sections via gaps between the irregular floor of the tank and the lower edges of the partitions. The four central sections held prawns during experiments. These sections were set out to be homogenous spaces with no apparent positive or negative stimuli (light, tidal flow, view of other prawns, flow of water-borne chemicals) in any direction. A line drawn down the centre of each section was a permanent marker for quantification of locomotor activity.

Experiments were recorded using a 24 h time-lapse video camera under a constant (red) lighting. The constant red light source, a 40W red light bulb, was required for filming in the otherwise dark room.

4.2.2. Behaviour experiments of *Palaemon affinis*

Four prawns were collected for each experiment from rock pools, other than the study site pool, at Point Kean, Kaikoura. The prawns were placed singly in a section of an experimental tide tank. Only the central four sections were used because, as noted above, these sections were designed to be homogenous (no boundary walls, similar lighting). The animals were acclimated to experimental conditions for 24-48 h before each experimental run.

4.2.2.1.Effect of tidal cycles on locomotor activity

The apparatus was used to test the null hypothesis that tide cycle has no effect on locomotor activity. Two separate experiments were run, in the first of which, a constant level of light, in addition to the red light used for filming, was provided, and a constant water temperature of 12 ± 1°C. In the second experiment the apparatus was illuminated by the red light only, to simulate darkness while allowing recording of activity, and at a constant water temperature of 20 ± 2.5°C. The pump was set to simulate the natural 25 h tide cycle for both experiments. Prawns were recorded on videotape for a complete 25 h tide cycle. Carapace length (CL), total body length

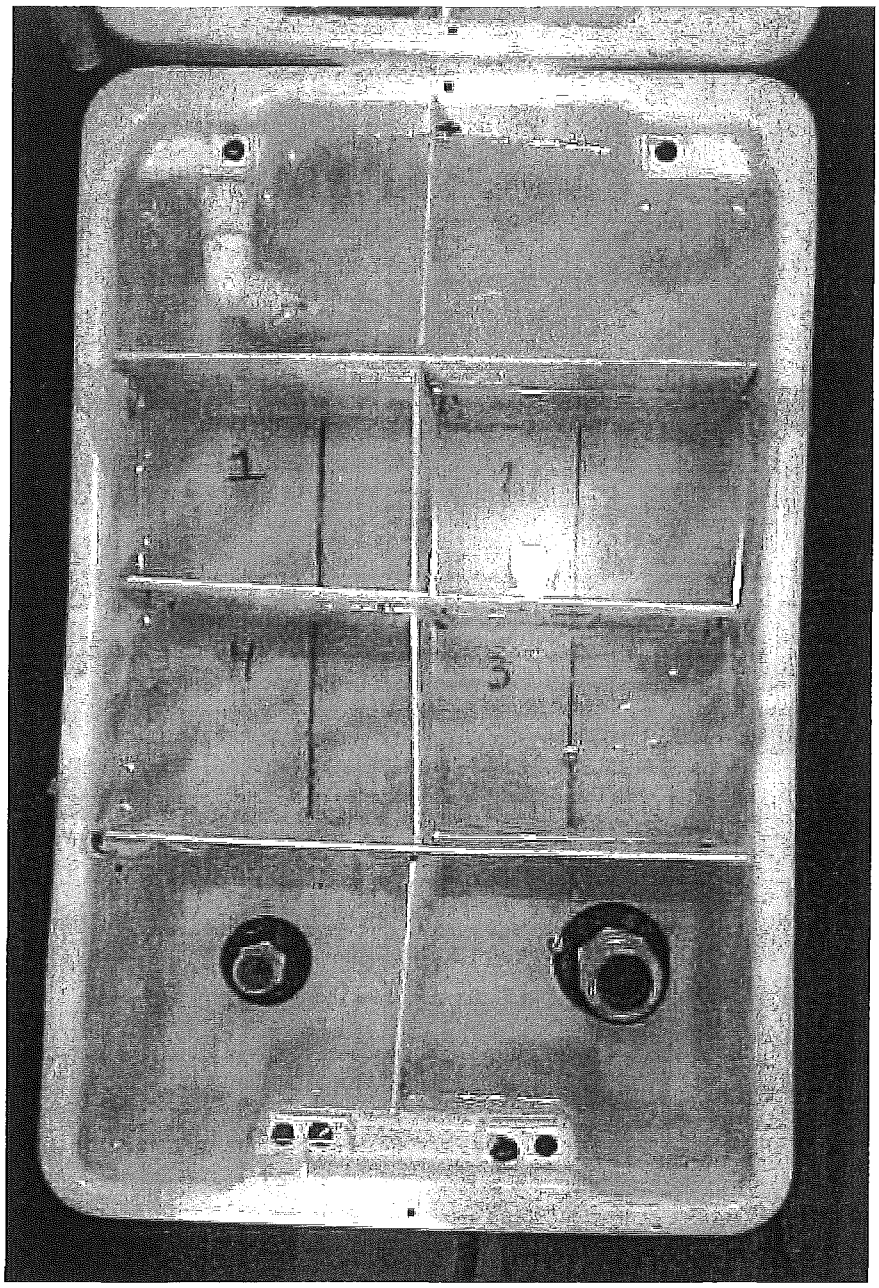


Plate 4.2 Experimental tide tank in an enclosed room at the Edward Percival Field Station, Kaikoura, in 2000. Tank divided into eight sections, with the central four used for prawn experiments, as they were homogeneous spaces. Central lines drawn in each of the four sections to quantify locomotor activity.

(TBL), wet weight (W) and sex were recorded for each prawn after each experiment was concluded. Each prawn was used only once. The videotapes were viewed and the activity levels were quantified by counting the numbers of times a prawn crossed over the centrally marked line during the period of analysis chosen (6 equal periods of 1 h 2.5 min each). Data were expressed as percentages of total activity (locomotor) for periods and tidal states. Male and female prawns were used in all experiments except the control. As sex was determined from external morphology, individuals could not be sexed before experiments. However, no differences were found in the locomotor (and feeding) activity between the sexes, so it was assumed that using a single sex (all female) for the controls did not affect the results.

4.2.2.2.Effect of light cycles on locomotor activity

The null hypothesis that light has no effect on locomotor activity was tested using a 12 h light: 12 h dark regime, with the 12 h light beginning at 0800 and ending at 2000. The experiment was done at a water temperature of 14.5 ± 2°C and at a constant low tide (7 cm water depth). Prawns were video-recorded for a 24 h light:dark cycle. Carapace length (CL), total body length (TBL), wet weight (W) and sex were recorded for each prawn after each experiment. Activity levels were assessed as for the tidal experiments, except sample periods were 1 h (instead of 1 h 2.5 min) and light phases (12 h light: 12 h dark); the number of times a prawn crossed the central line was counted for each period (1h) and light phase.

4.2.2.3.Control for the effects of tide and light on locomotor activity

To test for artefacts within the locomotor activity experiments, animals were observed under constant darkness (red light only) with no change in tide. The experiment was done at a water temperature of 10 ± 2°C. Prawns were video-recorded for a 25 h period. Carapace length (CL), total body length (TBL), wet weight (W) and sex were recorded for each prawn at the conclusion of the experiment. Activity levels were assessed as for the tidal and light experiment: the number of times a prawn crossed the central line was counted for each 1 h 2.5 min period.

4.2.2.4.Effect of tidal and light cycles on feeding activity

The null hypothesis that tide and light have no effect on feeding activity was tested by experiments using a natural 25 h tide cycle together with a 12 h light: 12 h dark regime. Water temperature was maintained at 19.5 ± 1.5°C and red light was used throughout the experiment to allow for video recording during the 12 h period of the dark cycle. Prawns were starved for 3 days before filming, with recording starting on the 4th day when a piece of raw fish was placed in the centre of the tank at the beginning of the "low tide". The fish flesh was removed and replaced with a fresh piece of fish at the beginning of every tide for the duration of the experiment. Carapace length (CL), total body length (TBL), wet weight (W) and sex were recorded for each prawn after each experiment. Each prawn was used for only one experiment.

Feeding activity was quantified by counting the number of times the prawn settled on the piece of fish during each period (1 h 2.5 min). If the prawn remained on the fish flesh for >2 min, the prawn was scored a point for each minute it remained on the fish. The first high and first low tides were not included in the statistical analysis because of the significantly higher feeding activity after the period of starvation.

4.2.3. Statistical analysis

Statistical analysis was done using software STATISTICA® or PRISM®. All data were tested for deviations from Gaussian normality with the Kolmogorov-Smirnov (KS) test before any statistical analysis.

Locomotor and feeding activity were described by percentages of total activity for each period and tidal or light cycle. Percentages were arcsine-transformed before statistical analysis. Differences between periods were tested using analysis of variance (ANOVA) and between each tide or light phase using Student's *t*-tests.

4.3. Results

4.3.1. Effect of tidal cycles on locomotor activity

Equal numbers of male and female prawns (n=4) were used in the tidal experiment under constant light conditions. The mean size was 8.5 mm carapace length (CL), 23.25 mm total body length (TBL), and 0.1055 g wet weight (W). Likewise in the

tidal experiment under constant darkness, 1 male: 1 female prawns (n=4) were used; with prawns of a mean size of 10.25 mm CL, 27.25 mm TBL, and 0.653 g W. There was no difference in the behavioural patterns of male and female *Palaemon affinis*.

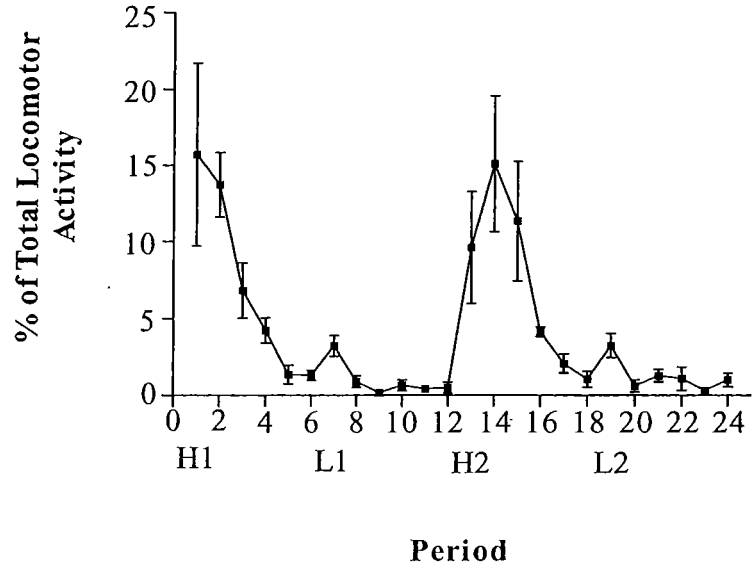
P. affinis locomotor activity showed a clear tidal rhythm under constant light (Fig. 4.1a). Locomotor activity was significantly greater (P<0.0001) during periods of high tide than during low tide, with peak locomotor activity (~15% of total activity) during one of the first two periods of each high tide (period 1 and 14). Activity declined dramatically in the remaining high tide periods, and stayed low throughout the following low tide. However, there were small peaks of locomotor activity during the first period of each low tide (period 7 and 19) when the tidal flow was changing. The increased activity with the ebb of the tide could have the resulted from the prawns searching for shelter, as the experimental tanks offered none. In addition, after the tidal change was completed and the water was still, the prawns ceased their activity and pressed their bodies against the wall, generally remaining there until the next tidal change.

Locomotor activity during high tides accounted for ~ 90% of all *P. affinis* locomotor activity under constant light, with nearly half (44.9 ± 6.4%) observed during the first high tide (H1), and the rest (45.2 ± 6.7%) during the second high tide (H2). This pattern was significantly different (P<0.0001) from the pattern of activity during both low tides (L1=5.9 ± 1.3% and L2=7.6 ± 0.8%) (Fig. 4.1b).

Rhythms of activity corresponding with the tidal state were still evident during constant darkness (Fig. 4.2a), but locomotor activity was significantly greater during periods of night-time high tide (P<0.0001), than at periods during daytime high tide and low tides. Peak locomotor activity (12.7 ± 4.3% of total activity) occurred during period 15, which was the third period of the second high tide (H2) and a time of expected night. Locomotor activity levels during periods in this tide were high, 4.4 ± 1.4% to 12.7 ± 4.3% of total activity, whereas during all other periods activity levels were only 0.9 ± 0.4% to 5.8 ± 3.5%.

Additionally, locomotor activity during the high tide at the time of expected night (H2) accounted for 57.6 ± 9.8% of total activity, which differed significantly (P=0.001) from activity during all other tides (Fig. 4.2b). Activity level during the high tide at the time of expected day (H1) was similar to those at both low tides, and

a)



b)

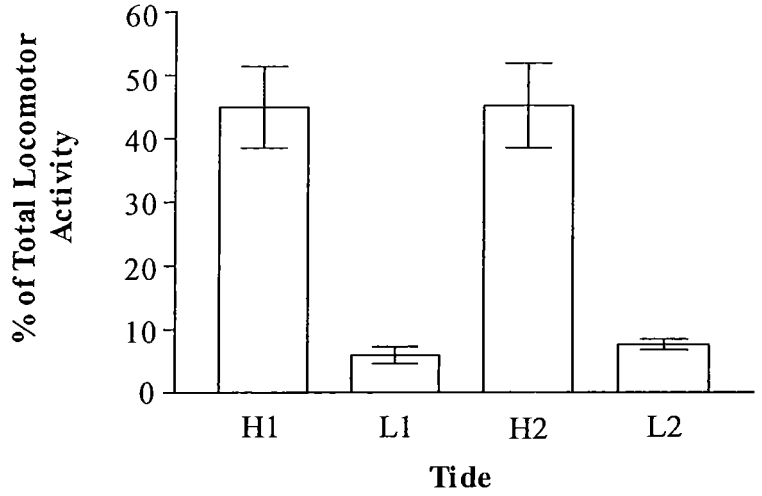
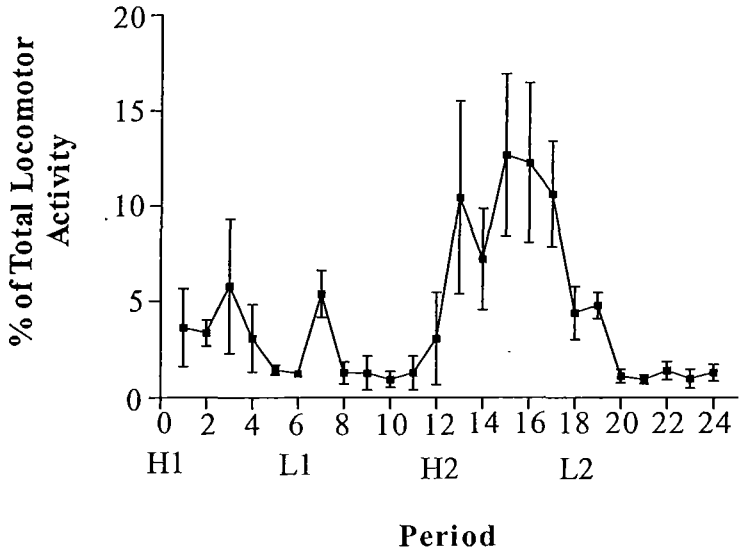


Fig. 4.1 Locomotor activity (% of total) of *Palaemon affinis* in experimental environment: a, per period (1 period = 1 h 2.5 min, with tidal changes every 6 periods beginning with high tide simulating natural tide cycle at Kaikoura) ($P<0.0001$); b, per 25 h tide cycle ($P<0.0001$). Error bars, ± 1 SE. H1, first high tide; L1, first low tide; H2, second high tide; L2, second low tide. Temperature 12 ± 1°C; constant light. accounted for only 18.8 ± 5.6% of total locomotor activity. Locomotor activity during the first low tide (L1) was 13.2 ± 5.8% and 10.6 ± 1.6% during the second low tide (L2).

a)



b)

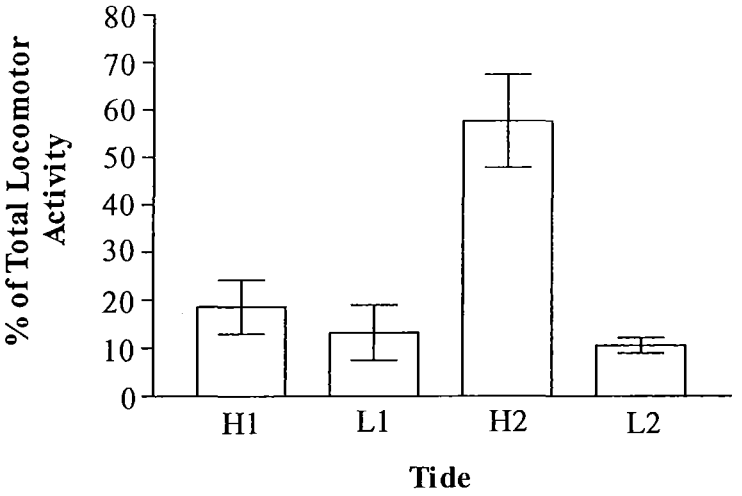


Fig. 4.2 Locomotor activity (% of total) of *Palaemon affinis* in experimental environment: a, per period (1 period = 1 h 2.5 min, with tidal changes every 6 periods beginning with high tide, simulating natural tide cycle at Kaikoura) ($P<0.0001$); b, per 25 h tide cycle ($P=0.001$). Error bars, ± 1 SE. H1, first high tide; L1, first low tide; H2, second high tide; L2, second low tide. Temperature 20 ± 2.5°C; constant darkness. Natural dark period was periods 8-19.

accounted for only 18.8 ± 5.6% of total locomotor activity. Locomotor activity during the first low tide (L1) was 13.2 ± 5.8% and 10.6 ± 1.6% during the second low tide (L2).

During preliminary experiments, water movement did not stimulate tidal-cycle rhythms in locomotor activity in *P. affinis*. Prawns were held in a tank under constant light with tidal variations that did not represent the natural tide cycle: the simulated tidal cycle was the inverse of the "expected" tidal cycle. Under such conditions, there were no patterns of activity in *P. affinis* in time with the induced tidal rhythms and their activity levels were similar throughout all periods of observation.

4.3.2. Effect of light cycles on locomotor activity

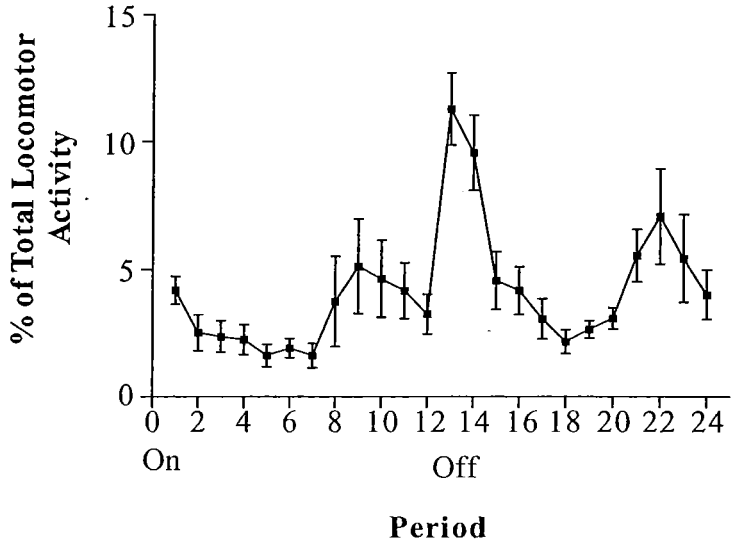
Two prawns (the largest male and female) used in the first light regime experiment moulted during filming. Data from the two moulted prawns were excluded from the analysis and the experiment was repeated with fresh animals. Data from the two non-moulted prawns were combined with the data from the second (n=6; 1:5 sex ratio). The mean size for the experimental animals was 9.7 mm CL, 25.8 mm TBL, and 0.132 g W. The single female had the largest body size (11 mm CL, 28 mm TBL) and weight (0.183 g) of the six prawns used. Again, there were no differences in the behavioural patterns of male and female *P. affinis*.

P. affinis exhibited a strong nocturnal rhythm of locomotor activity. Locomotor activity was significantly greater (P<0.001) during periods of darkness than during light. Peak locomotor activity, 11.3 ± 1.4% of total activity, occurred during the first period of darkness (period 13) (Fig. 4.3a), with general levels of activity also being greater during periods of darkness (2.2 ± 0.5% to 11.3 ± 1.4% of total locomotor activity), whereas activity levels during light periods were only 1.6 ± 0.4% to 5.1 ± 1.8% of the experimental total. As a whole, locomotor activity levels during the dark were significantly greater than during the light, and dark activity accounted for 65.8 ± 5.2% of total activity (P=0.0017) (Fig. 4.3b).

4.3.3. Control for the effects of tide and light on locomotor activity

All the prawns (n=4) used in the experimental control were female, with a mean size of 9.25 mm CL, 24.5 mm TBL, and 0.516 g W.

a)



b)

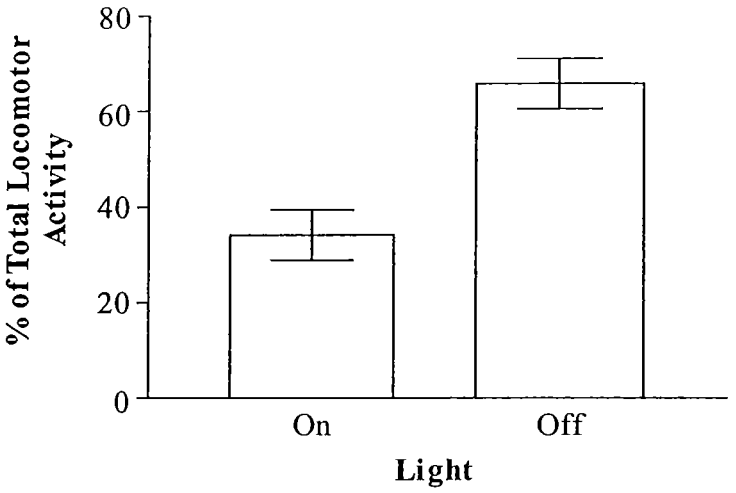


Fig. 4.3 Locomotor activity (% of total) of *Palaemon affinis* in experimental environment: a, per period, 1 period = 1 h, light changes every 12 hours beginning with light ($P<0.001$); b, per 24 h light cycle ($P=0.0017$). Error bars, ± 1 SE. On, light; Off, darkness. Temperature 14.5 ± 2°C; constant low tide.

There was no rhythm in the activity levels of *P. affinis* when the animals were kept in darkness with no tidal change (Fig. 4.4). Locomotor activity did not differ between periods regardless of the expected tidal state or light:dark phase, ranging from 0 to 15.4 ± 9.4% of total activity in all periods. However, it was interesting that the peak activity occurred during a period of expected dark and high tide (period 12). There was little or no activity during periods of expected daylight hours (period 1-5) which were also periods of expected low tide.

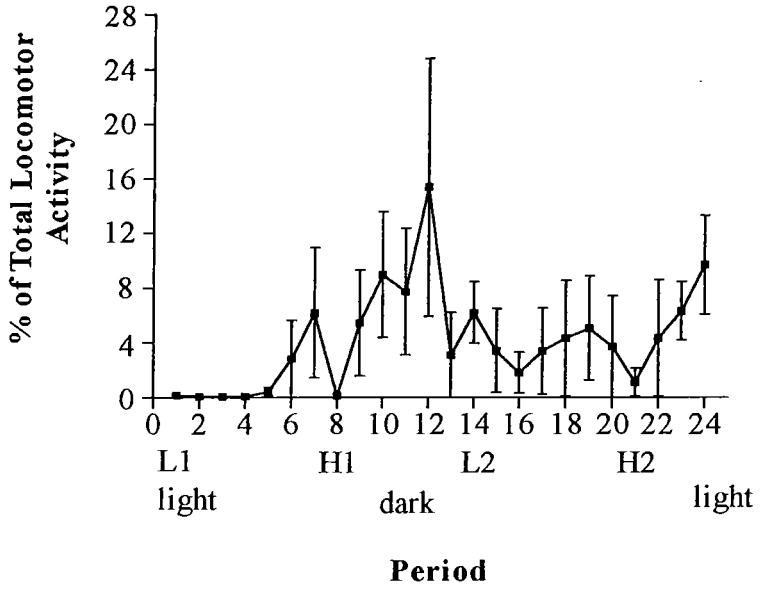


Fig. 4.4 Locomotor activity (% of total) of *Palaemon affinis* in experimental environment per 25 h cycle. Constant light and low tide (7 cm water depth). Temperature 10 ± 2°C. L1, expected low tide; H1, expected high tide; L2, expected low tide; H2, expected high tide. Expected light, periods 1-10, and 24; expected dark, periods 11-23.

4.3.4. Effects of tidal and light cycles on feeding activity

Two male and two female prawns (n=4) were used to test the effects of tidal and light cycles on feeding activity. The mean size of the animals was 10 mm CL, 27 mm TBL and 0.157 g W. Again, there were no differences in the behavioural patterns of the male and female *P. affinis*.

No diel or tidal rhythms were detected in the feeding activity of the *P. affinis* in the experiment (Fig. 4.5a). When food was always available, levels of feeding activity were similar throughout the light and tidal cycles. Activity levels during observation periods similarly ranged from 2.1 ± 0.5% to 15.5 ± 9.8% of total feeding activity, with peak feeding activity during a time of expected darkness and low tide (period 23). Likewise, feeding activity levels were similar through the tidal cycle, varying from 20.4 ± 2.4% to 31.9 ± 8.1% of total feeding activity regardless of tidal state (Fig. 4.5b). The maximum feeding activity occurred during the first low tide (L1), which was mainly during darkness.

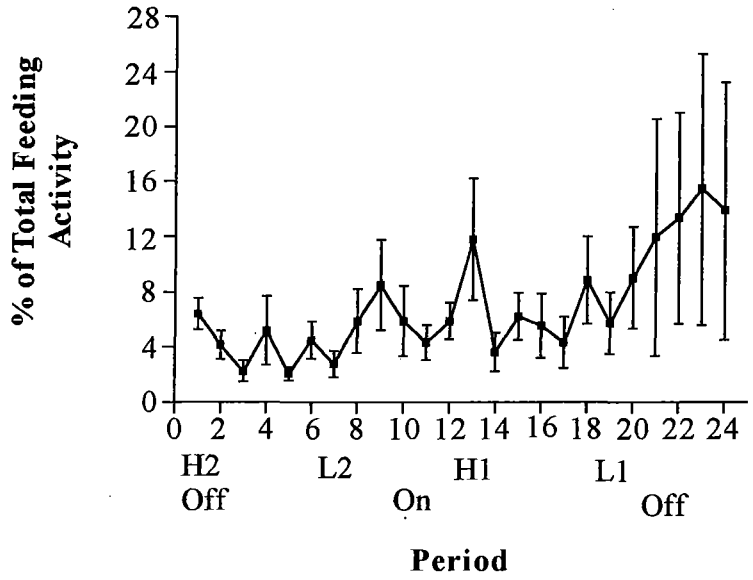
4.4. Discussion

4.4.1. Timing of locomotor activity in *Palaemon affinis*

Palaemon affinis locomotor activity showed both circatidal and diel exogenous rhythms with maximum activity at high tide and at night. Water movement alone was not enough to stimulate circatidal rhythms in *P. affinis*, as was observed in a preliminary experiment when prawns were held under tidal changes which were the inverse of the "expected" tidal cycle, and constant light. The lack of an activity pattern in time with the tidal rhythm in the preliminary experiment may have been because tidal rhythms are partially exogenous and partly entrained in *P. affinis*. For example, Rodriguez & Naylor (1972) found the locomotor activities in *Palaemon elegans* Rathke and *P. serratus* Pennant were controlled by an endogenous tidal component, but persisted only for ~ 48 h under constant conditions. If *P. affinis* exhibited similar patterns, an endogenous tidal rhythm may not have been detected because the prawns used in the experimental control were acclimatised for 24-48 h before filming began.

Alternatively, synchronisation of activity with tidal rhythms may result from the combination of water movement and other, unknown, variables. Rodriguez & Naylor (1972) reported that light:dark phases may be an important synchroniser of tidal rhythms in *Palaemon elegans* and *P. serratus* locomotor activity. Certainly light was an important factor driving the periodicity of *P. affinis* locomotor activity. If the combination of light:dark phases and water movement synchronise exogenous tidal rhythms of *P. affinis* locomotor activity, rhythms may not have been detected in the

a)



b)

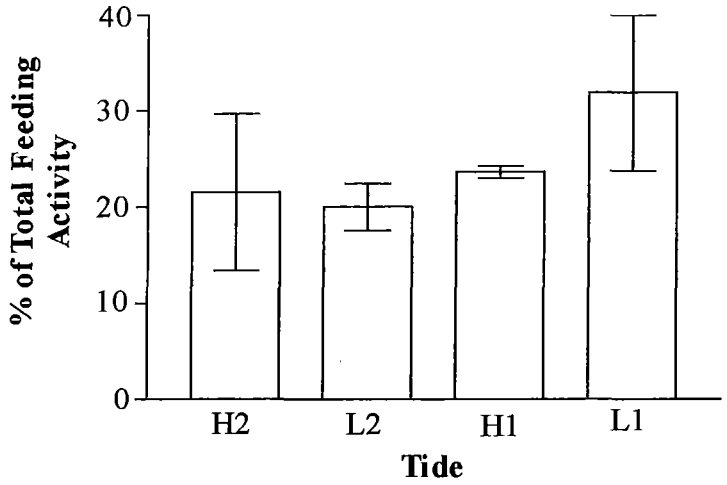


Fig. 4.5 Feeding activity (% of total) of *Palaemon affinis* in experimental environment per: a, period (1 period = 1 h 2.5 min, with tidal changes every 6 periods beginning with high tide, simulating the natural tide cycle at Kaikoura and light changes every 12 h beginning with darkness); and b, 25 h tide cycle. Error bars, ± 1 SE. H1, first high tide; L1, first low tide; H2, second high tide; L2, second low tide; Off, darkness; On, light. Temperature 19.5 ± 1.5°C.

preliminary experiment because neither "tidal" nor light cycles was set to simulate (or be in phase with) those of the natural environment at Kaikoura at the time.

A variety of rhythms controlling locomotor activity of species of *Palaemon* have been reported and the rhythms appear to be site dependent. For example, the rhythms controlling the locomotor activity of *P. serratus* differed between studies. Guerao & Ribera (1996) found that the locomotor activity of *P. serratus* from a non-intertidal habitat in Alfacs Bay, Ebro Delta, Spain was controlled by an endogenous circadian rhythm, with no apparent circatidal rhythm. Conversely, the locomotor activity of *P. serratus* from an intertidal habitat in South Wales was controlled by an endogenous tidal component, with the day:night cycle possibly synchronising the activity with the tidal rhythm (Rodriguez & Naylor 1972). Forster (1951) observed both tidal and diel rhythms of migrations up and down the shore in an intertidal population of *P. serratus* from Plymouth, UK.

In general, the locomotor activities of *Palaemon* species appear to be controlled by light:dark cycles, with maximum activity at night. Light controlled, at least in part, the locomotor activity of *P. xiphias* (Guerao 1995), *P. elegans* (Rodriguez & Naylor 1972), *P. serratus* (Forster 1951; Rodriguez & Naylor 1972; Guerao & Ribera 1996), *P. longirostris* (Fincham & Furlong 1984), *P. adspersus* (Jansson & Källander 1968; Inyang 1978; Hagerman & Ostrup 1980), and *P. affinis* (present study), regardless whether the animals were living in an intertidal or non-intertidal habitat.

Many authors have suggested that the nocturnal behaviour of *Palaemon* species is a consequence of the need to avoid predators because they are an important food source for a range of fish species (Forster 1951; Rodriguez & Naylor 1972; Guerao 1995; Guerao & Ribera 1996). However, this interpretation of a widespread and important activity in *Palaemon* species lacks supporting evidence for factors distinguishing between causes, consequences, and the controlling rhythm. Further research focusing on correlations between predator avoidance and the periodicity of locomotor activity in *Palaemon* species would be necessary to determine the causes and effects of the observed diel rhythms in activity.

In contrast, the importance of circatidal rhythms appears to be limited, as might be expected, to intertidal populations. Only *Palaemon serratus* populations

from intertidal habitats have been observed to have circatidal rhythms (Forster 1951; Rodriguez & Naylor 1972), as did intertidal *P. elegans* (Rodriguez & Naylor 1972) and *P. affinis* (present study).

Circatidal rhythms may be important for maintaining an appropriate habitat in a constantly, but predictably, changing environment. Activity levels entrained to tidal cycles would ensure that mobile intertidal species move up and down the shore with the changing tide to avoid exposure at low tide (Rodriguez & Naylor 1972; Guerao & Ribera 1996). However, it is interesting that circatidal rhythms may also in part control reproductive effort in female *Palaemon longirostris* (Fincham & Furlong 1984). Fincham & Furlong (1984) found that the swimming activity of non-ovigerous female *P. longirostris* was controlled by a circadian rhythm, but when the ovaries began to ripen, a weaker circatidal rhythm became apparent. This then ceased once the female became ovigerous. Fincham & Furlong (1984) suggested that the additional circatidal rhythm may be related to the necessity to mate, and that the risk involved in swimming during daylight might be outweighed by the benefits of ensuring reproductive success. However, as with diel rhythms, further work is needed on circatidal rhythms in relation to other environmental and biological factors before the origin and mechanisms that maintain circatidal rhythms are understood.

4.4.2. Timing of feeding activity in *Palaemon affinis*

Tidal and light cycles did not affect *Palaemon affinis* feeding activity when food was constantly available, which suggests that other variables, such as food abundance or level of satiety or hunger, may control feeding activity in this species. Literature searches revealed little information on factors controlling feeding activity, including the actual feeding period, of *Palaemon* species, but evidence suggests that most species of *Palaemon* are nocturnal feeders. This conclusion is, however, based on extrapolation of results from locomotor activity experiments and stomach content analysis. For example, *P. adspersus* (Hagerman & Ostrup 1980), *P. xiphias* (Guerao 1995) and *P. serratus* (Guerao & Ribera 1996) show nocturnal activity patterns. Inyang (1978) reported that most empty *P. adspersus* stomachs (80% of the empty 30%) were from specimens collected after midday and suggested this may result from feeding activity during night and the evacuation of prey remains during the morning.

Likewise, Guerao (1995) found high stomach fullness values in *P. xiphias* collected at dawn, as did Guerao & Ribera (1996) for *P. serratus*. However neither study reported fullness values for specimens of either species collected at times other than dawn. Guerao (1995) and Guerao & Ribera (1996) also suggested the high stomach fullness values might result from both species feeding at night.

As with other species of *Palaemon* for which data are available, locomotor activity in *P. affinis* showed diel rhythms, with increased activity at times of night and low fullness values in stomachs collected after midday. However, these data are insufficient to prove that *P. affinis* is a nocturnal feeder. The laboratory experiments suggested that the diel rhythms controlling locomotor activity in *P. affinis* were exogenous. Individuals of *P. affinis* showed similar levels of activity when under constant light, which suggests that *P. affinis* can quickly adapt to changes in its environment, even those that are entirely unnatural.

In addition, low fullness values in *P. affinis* stomachs could also result from the killing and preservation methods adopted in this study: Forster (1951) suggested animals placed live into formalin usually expelled their stomach contents. One point that may be important is that the digestion rate in *P. affinis* stomachs may be slow. Trials of stomach content analysis were done on prawns from the tidal experiments to determine if live animals placed in formalin did expel their stomach contents. Although the results were inconclusive, I did find that *P. affinis* held in a tank without food for 4 days still retained stomach contents. Furthermore, two of the stomachs were 100% full, which suggests that digestion may take longer than 4 days in *P. affinis*. Three of four stomachs examined contained pieces of amphipod, and one stomach contained sponge spicules and a small amount of plant material, none of which could have been ingested in the experimental tank.

The apparent lack of diel or circatidal rhythms controlling *P. affinis* feeding activity means that feeding levels were similar throughout all periods when food was available. These observations suggest that *P. affinis* will feed whenever food is available regardless of tidal or light phases. This is not surprising if the species is an opportunistic predator that often lives in unpredictable habitats such as tide pools. Results from this study further suggest that *P. affinis* is an opportunistic predator that feeds primarily on gammarid amphipods. Predators can, in general, be expected to be

adapted to the environmental conditions of the habitat occupied by its prey (Barnes & Hughes 1982) rather than be limited to a restricted habitat themselves. If this is so for *P. affinis*, many behavioural patterns exhibited by the prawn may be in response to selection for individuals whose behaviours match various aspects of the biology of gammarid amphipods, including the time of their feeding activity. Further research is needed on the relationship between *P. affinis* and gammarid amphipods to better understand *P. affinis* feeding activity.

Chapter Five

General Discussion

Chapter Five: General Discussion

5.1. Feeding biology

Palaemon affinis belongs to the largest and most successful order of Crustacea, Decapoda, which contains about 8,500 species. The Decapoda are divided into two suborders, the Natantia ("swimming decapods", with ~ 2,000 species) and the Reptantia ("crawling decapods"). Species of *Palaemon* are natant prawns belonging to the Caridea, the more diverse of the two sections of Natantia (Brusca & Brusca 1990).

As with most natant decapods, many species of *Palaemon* are considered to be predators (Sitts & Knight 1979; Guerao 1995; Guerao & Ribera 1996); while others are omnivores that include crustaceans in their diet (Forster 1951; Subrahmanyam 1974; Inyang 1978). Morton & Miller (1968) and Jones (1983) suggested that *P. affinis* is a scavenger, but the results of the present study suggest that *P. affinis* is primarily a carnivore, preying mainly upon gammarid amphipods. Other items, including unidentifiable matter, plant material, polychaetes, isopods, ostracods, sand grains, sponge spicules, and crab were present in the diet of *P. affinis* from all three sites, but in much lesser amounts. Molluscs were present only in prawns from Taylors Mistake, where the abundance of gammarid amphipods was more variable than at the other two sites.

Predators can be expected to be adapted to the environmental conditions in the habitat of their prey. In addition, predators show a wide range of feeding behaviours, from specialist to generalist, which are considered adaptations to prey abundance. Predators that feed on prey whose abundance varies unpredictably are typically generalists that alter their diet in response to changes in the relative abundance of their preferred prey. Generalists also spend most of their foraging time locating prey, feeding opportunistically on easily caught prey, and taking carrion (Barnes & Hughes 1982).

5.2. Distribution patterns

Species of *Palaemon* occur world-wide in almost all aquatic habitats. *P. affinis* in this study were found in two different New Zealand intertidal habitats – rock pools and an estuarine channel. Both of these are common habitats for many species of *Palaemon*

(Forster 1951; Sitts & Knight 1979; Attrill & Thomas 1996), but they are not confined to them. Some species also occur in shallow seagrass meadows in the Spanish Mediterranean (e.g., Guerao & Ribera 2000), on sandy mud flats near mangrove areas and in freshwater habitats in Brazil (Anger & Moreira 1998). Obviously, environmental factors, salinity in particular, vary widely between these habitats and even within the same habitats at different stages of the tide. This suggests that the distribution of *Palaemon* may not be limited by environmental variables such as salinity. Most species of *Palaemon* are highly tolerant of salinity changes, with the reported tolerances in most ranging from 1‰ to over 40‰ (Kirkpatrick 1981). *P. affinis* can survive salinities of 5-43‰ (Kirkpatrick 1981; Kirkpatrick & Jones 1985).

Species of *Palaemon* occur on rock or mud substrata, and possibly in algal beds, and these features of their habitat could determine the distribution of *Palaemon* species. However, the environmental factors assessed in this study – water depth (minimum/maximum), water temperature, salinity, type of substratum, and size of habitat – showed little correlation with the composition of individual *P. affinis* communities. The exception was Taylors Mistake, where salinity was closely related (~89% similarity) to the community composition. The environmental variables best matching the changes between *P. affinis* community compositions were the type of substratum, however, the correlations were low (only ~ 50% similarity), which suggested that other unknown factors, possibly the distribution of prey, were determining the distribution of *P. affinis*. The broad distribution of *Palaemon* species may be limited in part to habitats with rock or mud substratum, as a result of the distribution of its prey, rather than changing environmental conditions, including salinity.

5.3. Population density

Seasonal fluctuations in the abundance of species of *Palaemon* are common, and have been attributed to migration by some authors (Forster 1951; Rodriguez & Naylor 1972; Bamber & Henderson 1994; Attrill & Thomas 1996; Guerao & Ribera 2000), but not by others (Rodriguez & Naylor 1972; Guerao & Ribera 1996). Migratory behaviour may result from an intolerance to changes in certain environmental factors

(e.g., salinity or water temperature), as well as in response to biological factors, such as food abundance and the requirements of reproduction (Barnes & Hughes 1982; Guerao & Ribera 2000). *Palaemon* species exhibit a wide range of seasonal patterns in abundance, and the patterns appear to be species, and possibly population, dependent. Rodriguez & Naylor (1972) found that seasonal patterns in abundance differed in *Palaemon elegans* and *P. serratus* from rock pools in South Wales. They suggested that seasonal changes in the abundance of *P. elegans* might have resulted from seasonal differences in recruitment, as the species were consistently collected in pools high on shore throughout the year. In contrast, however, changes in *P. serratus* abundance may have resulted from migration to deeper waters to avoid cooler water temperatures in winter, as they were only collected in pools lower on shore in summer (Rodriguez & Naylor 1972).

Bamber & Henderson (1994) suggested that changes in the abundance of *P. serratus* of a small resident population in the Severn Estuary resulted from the addition of new recruits, and that larger individuals migrated to deeper waters in response to changes in salinity. Both studies, Rodriguez & Naylor (1972) and Bamber & Henderson (1994), suggested that the seasonal patterns of *P. serratus* abundance result from limitations to physical environmental factors, but neither confirmed the relationship.

Fluctuations in the abundance of *P. affinis* differed between populations. *P. affinis* were collected consistently from the Kaikoura pool, which suggests that the changes in abundance may have resulted from mortality, recruitment or migration. However, the prawns were not always collected at Taylors Mistake or the Culvert. The absence of *P. affinis* in samples from these two sites may have resulted from differences in efficacy of the sampling method or possibly from the prawns following the movement of their prey; which is a common behaviour in predators (Barnes & Hughes 1982).

5.4. Growth and reproduction

In Crustacea, the hard exoskeleton and the necessity to moult limit both growth and reproduction (Hartnoll 1985). Sexual differences in growth and adult size are common in some *Palaemon* species (Forster 1951; Guerao *et al.* 1994; Guerao &

Ribera 2000). It has been suggested that differences in the growth of male and female *Palaemon* species result from predation pressure (Guerao *et al.* 1994). For example, male and female *P. xiphias* differ in their growth rates, and Guerao *et al.* (1994) suggest that the differences may result from males investing less energy into growth to decrease their risk to predation by fish. Reducing the female body size beyond a limit may not be beneficial as the total body length of female *P. xiphias* is correlated with fecundity. In other *Palaemon* species, males and females show differences in growth rates (Forster 1951; Guerao & Ribera 2000), which contrasts with *P. affinis*. Sexual dimorphism in *P. affinis* occurred in maximum body size, and not growth rate. Also, it is interesting that male and female *P. affinis* were the same size for most of the year and significant differences were not apparent until the breeding season, when females were larger than the males.

Reproduction in *Palaemon* occurs in all seasons and appears to be site dependent. For example, ovigerous female *P. serratus* from a population in Plymouth, UK were found in winter to early spring (Forster 1951), whereas ovigerous females from a population in the Severn Estuary, UK were present only in spring (Bamber & Henderson 1994). In the Spanish Mediterranean ovigerous females were collected only in winter (Guerao & Ribera 2000). The breeding season in *P. affinis* was in late spring and summer and may have been related to water temperature or to a minimum temperature that was sustained for some period of time. Further investigation into the reproductive biology of *P. affinis* is needed to determine which environmental variables affect the breeding seasons in different populations, and why there might be differences in the breeding season in different habitats.

5.5. Behaviour

Behavioural patterns of *Palaemon* appear, as might be expected, to be highly adaptive to the environmental conditions in its habitat. Circatidal and diel rhythms are important in controlling the locomotor activity of several species of *Palaemon* (Forster 1951; Jansson & Källander 1968; Rodriguez & Naylor 1972; Inyang 1978; Hagerman & Ostrup 1980; Fincham & Furlong 1984; Guerao 1995; Guerao & Ribera 1996). As *Palaemon* prawns are considered to be mainly predators, behavioural

patterns (especially locomotor activity) may in part be determined by the demands of locating and catching its prey, as well as the demands of its environment which can include strong tidal currents and wave action during storms.

Interpretations of locomotor activity in species of *Palaemon* are generally speculative. The prawns generally exhibit patterns of locomotor activity that have diel rhythms, with maximum activity occurring at night. The night maximum activity has led to the suggestion that *Palaemon* are nocturnal feeders (Inyang 1978; Guerao 1995; Guerao & Ribera 1996). Other authors suggest that increased activity at night may result from predator avoidance during the day, as most fish species feeding on crustaceans are presumably visual predators (Forster 1951; Guerao 1995; Guerao & Ribera 1996).

Feeding activity in *P. affinis* was opportunistic. When food availability was held constant, *P. affinis* fed throughout a diel cycle regardless of light or tidal phases. This suggests that factors other than tidal state or time of day control the prawn's feeding activity. Prey availability as well as the presence of predators may affect the diel and circatidal rhythms that control locomotor activity in *Palaemon* species. However, causal factors cannot be determined on the data presented here alone. Further research is needed to investigate which of a range of many possible environmental factors may affect locomotor and feeding activities of *Palaemon* species.

5.6. Conclusion

The results of this study provide some basic biological and behavioural information on the prawn *Palaemon affinis*, which is one of the most characteristic intertidal animals on the New Zealand shore. *P. affinis* is an important opportunistic predator, and not a scavenger as has been suggested in previous literature. The prawn feeds primarily on gammarid amphipods, but can eat other prey. The distribution of *P. affinis* within a particular habitat may be more limited than was once thought because its distribution may be determined by the microdistribution of its prey, rather than environmental variables. The locomotor activity of *P. affinis* exhibits diel and circatidal rhythms, but its feeding activity may be related to prey abundance, as no rhythmicity was evident in its feeding behaviour when fed *ad libitum*.

As this was a preliminary investigation on the biology and behaviour of *P. affinis*, further work is obviously necessary. However, the results suggest that such work could yield important theoretical insights into the role of predation in the evolution of behaviour, physiology and reproduction in intertidal invertebrates.

Acknowledgements

I would like to thank my supervisor, Dr. Islay Marsden, for her support in this research, most especially the reviewing of the manuscript.

Thank you also to Dr. Richard Holdaway for help with sampling. Thank you to Jack van Berkel for his clever ideas and for providing an extraordinary and professional facility in which to accomplish my work. Thank you to Dr. Graham Fenwick for help in the identification of amphipods. For technical support, thank you to: Eric Kopps, Wayne Nelson, Gavin Robinson, David Greenwood, Renny Bishop, Bruce Lingard, Franz Ditz, Graeme Bull, John Scott and Joanne Burke-Stewart, as well as to Hine Day, Trace Robinson, Lyn de Groot and Helen Spinks. A special thank you to Rosemary Knight for a lending ear. Thank you to Dr. Mike Hickford and John Perka for their help with statistical analysis.

Most especially I would to thank my family and friends for supporting my decision to return to university, especially one so far from home. It has been a wondrous experience in many respects. Thank you Sarah and John for your love and loyalty that pulled me through some of the roughest times. Thank you Darrick for the hours of laughter. Still wondering if you let the "cutelittlefish" out. My flatmates think I am nuts for laughing at that stupid song. Guess you need to be a Day to understand. Thank you Chris Muller for opening up your house as a bed & breakfast...lunch...dinner? It was much appreciated. Thank you Laura Boren for convincing him to do so. Also want to thank you Laura for your continual support and friendship. I hope you go far with the pinnipeds. Thank you Robert and Anne Boren as well for the lovely treats to Hislops and various other eateries, as well as to opening your home to me.

Special thanks to my flatmates for leaving me all the fairy cakes during the final throws of my thesis writing...and to Ann for baking them! Thank you Robyn Dunmore for the many hours of laughter and for being such a groovy flatmate, as well as to Sheba Mongrel for tolerating my stealing your squeaky toy, even though we all know you were annoyed. Thank you David Taylor for the clever idea of painting a light bulb red (children please don't attempt this at home) and the help with PRIMER®. Thank you Stacie Lillie for the never-ending chocolate sauce pudding (as

well as making me run it off afterwards) and the hours of sorting samples. Thank you Spencer Wood for brightening my day with new music (never to try to write a thesis on old CDs) and for the support you have given me over the last few months of my writing. I hope you enjoy Kaikoura and all the people who live here as much as I did. Finally, thank you Nichy Brown for help with formatting my final copy. Your logic and rationale saved me hours of frustration.

References

Anger, K., & Moreira, G.S. (1998). Morphometric and reproductive traits of tropical caridean shrimps. *Journal of Crustacean Biology* 18 (4): 823-838.

Attrill, M.J., & Thomas, R.M. (1996). Long-term distribution patterns of mobile estuarine invertebrates (Ctenophora, Cnidaria, Crustacea: Decapoda) in relation to hydrological parameters. *Marine Ecology Progress Series* 143: 25-36.

Ayling, T., & Cox, G. (1982). *Collins guide to the sea fishes of New Zealand.* Auckland: William Collins Publishers Ltd.

Bamber, R.N., & Henderson, P.A. (1994). Seasonality of caridean decapod and mysid distribution and movements within the Severn Estuary and Bristol Channel. *Biological Journal of the Linnean Society* 51: 83-91.

Barnes, R.S.K., & Hughes, R.N. (1982). *An introduction to marine ecology.* London: Blackwell Scientific Publications.

Bartholomew, G.A. (1977). Body temperature and energy metabolism. In: M.S. Gordon (Ed.). *Animal physiology: principles and adaptations*, 3rd ed. (pp. 364-449). London: Collier MacMillian.

Brusca, R.C., & Brusca, G.J. (1990). *Invertebrates.* Sunderland, MA: Sinauer Associates.

Campbell, P.J., & Jones, M.B. (1989). Osmoregulation of the estuarian prawn *Palaemon longirostris* (Caridea: Palaemonidae). *Journal of the Marine Biological Association of the United Kingdom* 69: 261-272.

Coleman, N. (1980). More on sorting benthic samples*. *Marine Pollution Bulletin* 11: 150-152.

Conan, G.Y. (1985). Periodicity and phasing of molting. In: A.M. Wenner (Ed.). *Factors in adult growth. Crustacean Issues* 3: 73-99. Boston: A.A. Balkema.

Corey, S., & Reid, D.M. (1991). Comparative fecundity of decapod crustaceans. I. The fecundity of thirty-three species of nine families of caridean shrimp. *Crustaceana* 60 (3): 270-294.

Cowey, C.B., & Forster, J.R.M. (1971). The essential amino-acid requirements of the prawn *Palaemon serratus*. The growth of prawns on diets containing proteins of different amino-acid compositions. *Marine Biology* 10: 77-81.

Emmerson, W.D. (1985). Fecundity, larval rearing and laboratory growth of *Palaemon pacificus* (Stimpson) (Decapoda, Palaemonidae). *Crustaceana* 49 (3): 277-289.

Fauchald, K. (1977). The polychaete worms: Definitions and keys to orders, families and genera. *Natural History Museum of Los Angeles County, Science Series* 28: 1-190.

Fincham, A.A., & Furlong, J.A. (1984). Seasonal swimming rhythms of female palaemonid estuarine prawns and shrimps. *Journal of Natural History* 18: 425-439.

Florkin, M (1960). Ecology and Metabolism. In: T. H. Waterman (Ed.) *The physiology of Crustacea. Volume 1: Metabolism and growth* (pp. 141-159). New York and London: Academic Press Inc.

Forster, G.R. (1951). The biology of the common prawn, *Leander serratus* Pennant. *Journal of the Marine Biological Association* 30 (2): 333-360.

Green, J. (1961). *A biology of Crustacea.* London: H.F. & G. Witherby Ltd.

Guerao, G. (1995). Locomotor activity patterns and feeding habits in the prawn *Palaemon xiphias* (Crustacea: Decapoda: Palaemonidae) in Alfacs Bay, Ebro Delta (northwest Mediterranean). *Marine Biology* 122: 115-119.

Guerao, G., & Ribera, C. (1996). Locomotor activity patterns and feeding habits in the prawn, *Palaemon serratus* (Pennant, 1777) (Decapoda, Palaemonidae) in the Alfacs Bay, Ebro Delta, Spain. *Crustaceana* 69 (1): 101-112.

Guerao, G., & Ribera, C. (2000). Population characteristics of the prawn *Palaemon serratus* (Decapoda: Palaemonidae) in a shallow Mediterranean bay. *Crustaceana* 73 (4): 459-468.

Guerao, G., Pérez-Baquera, J., & Ribera, C. (1994). Growth and reproductive biology of *Palaemon xiphias* Risso, 1816 (Decapoda: Caridae: Palaemonidae). *Journal of Crustacean Biology* 14 (2): 280-288.

Hagerman, L., & Ostrup, J. (1980). Seasonal and diel activity variations in the prawn *Palaemon adspersus* from a brackish, non-intertidal area. *Marine Ecology Progress Series* 2: 329-335.

Hardy, G.S. (1970). Circadian rhythms. *Tuatara* 18 (3): 124-131.

Hartnoll, R.G. (1985). Growth, sexual maturity and reproductive output. In: A. M. Wenner (Ed.). *Factors in adult growth. Crustacean Issues* 3: 101-128. Boston: A.A. Balkema.

Hartnoll, R.G., & Salama, A.J. (1992). The effect of protein source on the growth of the prawn *Palaemon elegans* Rathke, 1837 (Decapoda, Caridea). *Crustaceana* 63 (1): 81-90.

Holthuis, L.B. (1952). A general revision of the Palaemonidae (Crustacea Decapoda Natantia) of the Americas. II: the subfamily Palaemoninae. *Allan Hancock Foundation Occasional Papers* 12: 1-396.

Hyslop, E.J. (1980). Stomach content analysis – a review of methods and their application. *Journal of Fish Biology* 17: 411-429.

Inyang, N.M. (1978). Notes on food of the Baltic palaemonid shrimp, *Palaemon adspersus* var. *fabricii* (Rathke). *Meeresforschung: Reports on Marine Research* 26 (1-2): 42-46.

Jansson, B., & Källander, C. (1968). On the diurnal activity of some littoral peracarid crustaceans in the Baltic Sea. *Journal of Experimental Marine Biology and Ecology* 2: 24-36.

Jones, M.B. (1983). *Animals of the estuary shore: illustrated guide and ecology.* University of Canterbury Publication No. 32. University of Canterbury, Christchurch, New Zealand.

Kirk, R.M. (1977). Rates and forms of erosion on intertidal platforms at Kaikoura Peninsula, South Island, New Zealand. *New Zealand Journal of Geology and Geophysics* 20: 571-613.

Kirkpatrick, K. (1981). Salinity tolerance and osmoregulation of the New Zealand shrimp *Palaemon affinis* Milne Edwards, 1837 (Decapoda: Palaemonidae). Unpublished BSc with Honours thesis, University of Canterbury, Christchurch, New Zealand.

Kirkpatrick, K., & Jones, M.B. (1985). Salinity tolerance and osmoregulation of a prawn, *Palaemon affinis* Milne Edwards (Caridea: Palaemonidae). *Journal of Experimental Marine Biology and Ecology* 93: 61-70.

Knox, G.A. (1951). A guide to the families and genera of New Zealand polychaetes. *Tuatara* 4 (2): 63-85.

Knox, G.A. (Ed.). (1969). *The natural history of Canterbury.* Wellington: A.H. & A.W. Reed.

Knox, G.A., & Kilner, A.R. (1973). *The ecology of the Avon-Heathcote Estuary.* Unpublished Report to the Christchurch Drainage Board. The Estuarine Research Unit. University of Canterbury, Christchurch, New Zealand.

Kuun, P., Pakhomov, E.A., & McQuaid, C.D. (1999). Morphometric relationships of the caridean shrimp *Nauticaris marionis* Bate, 1888 at the Prince Edward Islands (Southern Ocean). *Polar Biology* 22 (3): 216-218.

Llodra, E.R., Tyler, P.A., & Copley, J.T.P. (2000). Reproductive biology of three caridean shrimp, *Rimicaris exoculata, Chorocaris chacei* and *Mirocaris fortunata* (Caridea: Decapoda), from hydrothermal vents. *Journal of the Marine Biological Association of the United Kingdom* 80: 473-484.

Marchand, J. (1981). Observations sur l'ecologie de *Crangon crangon* (Linné) et *Palaemon longirostris* H. Milne Edwards (Crustacea, Decapoda, Natantia) Estuarie Interne de la Loire (France). *Vie et Milieu* 31 (1): 83-92.

Marsden, I.D. (1981). *Marine biology of the Kaikoura Peninsula: quantitative intertidal survey.* Estuarine Research Report No. 25. University of Canterbury, Christchurch, New Zealand.

McDowall, R.M. (1969). Lunar rhythms in aquatic animals -a general review. *Tuatara* 17 (3): 133-144.

McGregor, D.D. (1964). Physical ecology of some New Zealand supralittoral pools. *Hydrobiologia* 25: 277-284.

McLay, C.L. (1988). Brachyura and crab-like Anomura of New Zealand. *Leigh Laboratory Bulletin*, No. 22. University of Auckland, Auckland, New Zealand.

McLay, C.L. (Ed.). (1995). *Keys to the marine invertebrates of the Kaikoura Peninsula: A laboratory manual.* Edward Percival Field Station, Zoology Department, University of Canterbury.

McLusky, D.S. (1971). *Ecology of estuaries.* London: Heinemann Educational Books Ltd.

McQueen, D.J., & McLay, C.L. (1983). How does the intertidal spider *Desis marina* (Hector) remain under water for such a long time? *New Zealand Journal of Zoology* 10 (4): 383-391.

Mees, J., & Jones, M.B. (1997). The hyperbenthos. *Oceanography and Marine Biology: an Annual Review* 35: 221-255.

Meglitsch, P.A. (1972). *Invertebrate zoology* (2nd ed.). New York: Oxford University Press.

Millward, W.A.M. (1975). *Physical characteristics of an estuarine environment.* Unpublished MA thesis, University of Canterbury, Christchurch, New Zealand.

Morton, J., & Miller, M. (1968). *The New Zealand sea shore.* Great Britain: C. Tingling & Co. Ltd.

Owen, S.J. (Ed.). (1992). *The estuary: where our rivers meet the sea. Christchurch's Avon-Heathcote Estuary and Brooklands Lagoon.* Parks Unit, Christchurch City Council.

Palmer, J.D. (1995). *The biological rhythms and clocks of intertidal animals.* New York: Oxford University Press.

Powell, A.W.B. (1979). *New Zealand Mollusca*: marine, land and freshwater shells. Auckland: Collins.

Primavera, J.H., Parado-Estepa, F.D., & Lebata, J.L. (1998). Morphometric relationship of length and weight of giant prawn *Penaeus monodon* according to life stage, sex and source. *Aquaculture* 164: 67-75.

Ra'anan, Z., & Cohen, D. (1985). Ontogeny of social structure and population dynamics in the giant freshwater prawn, *Macrobrachium rosenbergii* (de Man). In: A. M. Wenner (Ed.). *Factors in Adult Growth. Crustacean Issues* 3: 277-311. Boston: A.A. Balkema.

Richardson, L.R, & Yaldwyn, J.C. (1958). A guide to the natant Decapod Crustacea of New Zealand. *Tuatara* 7: 17-41.

Rodriguez, G., & Naylor, E. (1972). Behavioural rhythms in littoral prawns. *Journal of the Marine Biological Association of the UK* 52: 81-95.

Seed R., & Hughes, R.N. (1995). Criteria for prey selection in molluscivorous crabs with contrasting claw morphologies. *Journal of Experimental Biology and Ecology* 193: 177-195.

Sitts, R.M., & Knight, A.W. (1979). Predation by the estuarine shrimps *Crangon franciscorum* Stimpson and *Palaemon macrodactylus* Rathbun. *Biological Bulletin* 156: 356-368.

Stearns, S.C. (1976). Life-history tactics: A review of the ideas. *The Quarterly Review of Biology* 51: 3-47.

Subrahmanyam, M. (1975). Notes on some aspects of the biology of *Palaemon styliferus* Milne-Edwards from the Godavari estuarine system. *Journal of the Bombay Natural History Society* 72 (3): 683-691.

Tamaki, A., Ingole, B., Ikebe, K., Muramatsu, K., Taka, M., & Tanaka, M. (1997). Life history of the ghost shrimp, *Callianassa japonica* Ortmann (Decapoda: Thalassinidea), on an intertidal sandflat in western Kyushu, Japan. *Journal of Experimental Marine Biology and Ecology* 210: 223-250.

Walsh, L.J., & Mitchell, B.D. (1998). Factors associated with variations in abundance of epifaunal caridean shrimps between and within estuarine seagrass meadows. *Marine and Freshwater Research* 49: 769-777.

Waterman, T.H., & Chace, F.A., Jr. (1960). General crustacean biology. In: T. H. Waterman (Ed.). *The physiology of Crustacea. Volume 1: Metabolism and Growth* (pp. 1-33). New York and London: Academic Press Inc.

Webb, B.F. (1972). Fish populations of the Avon-Heathcote Estuary. 1. General ecology, distribution, and length-frequency. *New Zealand Journal of Marine and Freshwater Research* 6 (4): 570-601.

Webb, B.F. (1973). Fish populations of the Avon-Heathcote Estuary. 3. Gut contents. *New Zealand Journal of Marine and Freshwater Research* 7 (3): 223-234.

Wenner, A.M. (1972). Sex ratio as a function of size in marine Crustacea. *American Naturalist* 106: 321-350.

Williams, M.J. (1981). Methods for analysis of natural diet in portunid crabs (Crustacea: Decapoda: Portunidae). *Journal of Experimental Marine Biology and Ecology* 52: 103-113.

Woods, M.C., & Schiel, D.R. (1997). Use of seagrass *Zostera novazelandica* (Setchell, 1933) as habitat and food by the crab *Macropthalmus hirtipes* (Heller, 1862) (Brachyura: Ocypodidae) on rocky intertidal platforms in Southern New Zealand. *Journal of Experimental Marine Biology and Ecology* 214: 49-65.

Yaldwyn, J.C. (1954). Studies on *Palaemon affinis* M.—Edw. 1837, (Crustacea, Decapoda, Natantia.). Part I. Synonomy and external morphology*. *Transactions of the Royal Society of New Zealand* 82 (Part 1): 169-187.